

**Competition between perch  
(*Perca fluviatilis*) and roach  
(*Rutilus rutilus*) in south  
Swedish lakes**

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COMPETITION BETWEEN PERCH (*Perca fluviatilis*)  
AND ROACH (*Rutilus rutilus*) IN SOUTH SWEDISH LAKES

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## LIST OF PAPERS

The thesis is based on the following papers:

- I. Lessmark, O. Effects of temperature and weight on food consumption, food conversion and growth of perch (Perca fluviatilis) fed maximum rations.
- II. Lessmark, O. Effects of ration size and temperature on growth and food conversion of perch (Perca fluviatilis).
- III. Lessmark, O. Effects of temperature and weight on food consumption, food conversion and growth of roach (Rutilus rutilus) fed maximum rations.
- IV. Lessmark, O. Effects of ration size and temperature on growth and food conversion of roach (Rutilus rutilus).
- V. Lessmark, O. The combined effects of temperature, food quantity and food quality on interspecific competition between perch (Perca fluviatilis) and roach (Rutilus rutilus).
- VI. Lessmark, O. The utilization of plant material for metabolism and growth by roach (Rutilus rutilus).
- VII. Lessmark, O. Selective zooplankton predation by perch and roach.  
-Experimental studies on interspecific competition.
- VIII. Lessmark, O. Influence of abiotic and biotic factors on the structure of perch and roach populations in thirteen Swedish lakes, with special reference to interspecific competition.



## INTRODUCTION

Increasing interest has been focused on the influence of fish on other organisms since it has been demonstrated that fish strongly may affect species composition and biomass of phyto- and zooplankton as well as other biotic conditions and concentration of nutrients in lakes (Hrbacek et al. 1961, Andersson et al. 1978). More eutrophic conditions are created by dense fish populations compared to sparse. Various fish species have widely different effects on zooplankton (Nilsson and Pejler 1973) and other biotic and abiotic conditions in lakes. The structure of fish communities is determined by interspecific interactions between fish (Svärdson 1976). Competition between fish species may thus affect the structure of both the fish populations, and the populations of other organisms on different trophic levels, as well as affecting the physical and chemical conditions in lakes.

## BACKGROUND

Around 1970 I noticed that the perch populations in two lakes where perch and roach dominated, increased rapidly as the roach populations declined (Lessmark 1976). Strong competition was evident as limited food resources were shared by these species. In Finnish lakes dominated by perch and roach, competition between the two species was also evident (Sumari 1971). Roach was generally more abundant than perch, but in lakes where roach was absent, perch had a higher biomass than in lakes where both species were present.

This information stimulated me to study the problem why roach generally tends to be a better competitor and in many lakes is more abundant than perch

## SUMMARY OF THE RESULTS

In laboratory experiments (4-24 °C) on maximum rations of animal food, perch consumed more food than equal sized roach at temperatures between 4 and 22 °C and grew faster than roach over the entire temperature range (paper I, III, V). The relative difference between the growth rates for perch and roach decreased as the temperature increased. Perch is thus adapted to lower temperatures than roach and temperature regime in Swedish lakes favours perch more than roach.

In a wide size-range of animal food rations, perch was a more



efficient food converter than roach (paper I-V). Perch is favoured over roach when animal food is abundant, because perch is physiologically adapted to consume more food and to utilize the food better.

However, competition for animal food is often severe. Perch has a strictly carnivorous diet, whereas roach is able to utilize vegetable food when animal food is in short supply (paper VIII). Roach prefer animal food however, and grow faster on an animal diet.

In laboratory experiments, roach consumed large amounts of the green algae Spirogyra, Enteromorpha and Mougeotia, the macrophyte Lemna minor, the blue-green alga Aphanizomenon flos-aquae and fresh detritus (paper VI). Only L.minor and the blue-green alga could be used for metabolism and growth because roach cannot efficiently digest hard plant material with cellulose-rich cell walls. Blue-green algae, with cell walls composed mainly of glycopeptide but no cellulose, resulted in a considerable growth, although less than on an animal diet. Energy gain from the macrophyte covered only partly metabolic demand.

Perch and roach were size selective when offered zooplankton of different sizes (paper VII). Roach was a more adept predator on small zooplankton than perch. The minimum prey size of perch was bigger than of equal sized roach. This is explained by differences between the two species as regards sight, foraging behaviour and energy expenditure per prey. Roach had difficulties capturing fast-moving copepods and elected immobile or slow-moving prey. Roach is described as a cropper, whereas perch behaves more like a hunter, consuming larger and more mobile prey. As roach is better able to make use of small zooplankton throughout its life span, a larger proportion of the zooplankton community is available to it as food compared with that available to perch. Furthermore, roach disfavors perch by reducing the size of zooplankton so much that they only can be used as food by the smallest perch. This is one of the reasons why roach is more abundant than perch in many lakes.

The structure of the perch and roach populations in 13 south Swedish lakes with widely differing limnological characteristics, was not directly related to any of the abiotic factors: lake area, depth, transparency or phosphorus concentration (paper VIII). Biotic factors were far more important. Blue-green algae were important as food and in lakes with high biomass of blue-greens the roach populations consisted of numerous and slow-growing fish with low mean-length and size-class diversity. Size of zooplankton was important

and the presence of big cladocerans was positively related to growth of perch and roach. The number of crustaceans, however, was insignificant for individual growth. Growth rates indicated severe food competition in all lakes except one.

Intraspecific competition for benthos between different-sized perch most negatively affected the largest benthos-feeding fish, and perch reached a bottle-neck situation at the change-over from benthos-feeding stage to piscivory.

Vegetable food became more important in the diet of roach when competition for animal food was strong. Intraspecific competition between different-sized roach was most severe to the largest fish. Their diet was more vegetarian than that of smaller fish.

Interspecific competition between perch and roach for benthos and zooplankton, had a negative effect on the growth and on the abundance of small perch, in the shallowest lakes. Perch and roach were the most dominant fish species and roach was more numerous than perch. The roach populations were mainly regulated by intra-specific competition. For perch, interspecific competition from roach was more important. In the deepest lakes, planktivorous small bream/white bream and vendace were abundant and were important food competitors, especially for roach.

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EFFECTS OF TEMPERATURE AND WEIGHT ON FOOD CONSUMPTION,  
FOOD CONVERSION AND GROWTH OF PERCH (*Perca fluviatilis*)  
FED MAXIMUM RATIONS.

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## SUMMARY

Perch (Perca fluviatilis) in the weight range 1-100 g were fed maximum rations of live Chaoborus larvae at the following temperatures: 4.0, 8.2, 12.2, 16.0, 20.0 and 24.0 °C. Maximum food consumption, food conversion and growth rate were dependent on temperature and on the weight of the fish. Optimum temperatures for food consumption, food conversion and growth declined with the increasing weight of the fishes. Maximum food consumption occurred at a higher temperature than maximum growth, which in turn occurred at a higher temperature than maximum food conversion. For a fish weighing 10 g the temperature for maximum consumption was above 24 °C, for maximum growth 24 °C and for maximum food conversion it was 17.5 °C.

## INTRODUCTION

Temperature is one of the most important abiotic factors regulating the success of a fish in its physical environment, because it influences the rate of vital processes like food consumption, food conversion, growth and activity. Different species are physiologically adapted to different temperatures. A better knowledge of the relation between energetics and temperature would contribute to a better understanding of fish ecology.

Growth and food consumption of perch have been correlated to temperature in several field studies (Le Cren 1958, Coble 1966, Neuman 1976, Craigh 1980). However, it has not been possible to estimate the extent to which growth is limited by temperature or by food, since the recorded growth rates have not been related to maximum growth rates at specific temperatures.

The aim of this study was to estimate how the maximum food consumption and food conversion and the maximum growth rate are influenced by temperature and by the weight of perch.

## METHODS

### Experimental set-up

Fish were taken by dipnet or electro fishing from Lake Sövdborgssjön in Scania, southern Sweden. They were acclimatized to experimental conditions for at least two weeks prior to the start of the experiments. During this time they were fed with dipteran larvae. The size range of the fish was 2.0-82.2 g. They were



divided into groups of as equal sized fish as possible with generally five individuals in each group.. The groups were kept in separate aquaria (60 l) with a constant through flow of water and a retention time of 1.5 h. The aquaria belonged to a semi-circulating system of 700 l with an 8 h renewal time for fresh water. The water was filtered and aerated before it was recirculated. The aquaria were cleaned and the faeces was removed at least once a day.

The experiments were performed at 4.0, 8.2, 12.2, 16.0, 20.0 and 24.0 °C with four groups of different sized fish at each temperature. At 28.0 °C only one experiment was run with only one group of equal-sized fish. The maximum temperature deviation in an experiment was  $\pm 0.2$  °C.

The experiments were run at different times of the year in an effort to follow the natural annual temperature cycle of the lake from which the fish originated (Tab. 1). Light regime was 18 h light and 6 h dark at temperatures from 28.0 to 12.2 °C and 12 h light and 12 h dark at 8.2 and 4.0 °C.

Prior to the start and end of an experiment the fish were starved to evacuate the gut content. The starving periods were different at the various temperatures, since the gut evacuation rate is regulated by temperature (Tab. 1).

Duration of the experiments was adjusted to temperature (Tab. 1). The experiments had to last long enough to result in a significant weight change but should not be longer than the obtained growth rates could be correlated to a specific fish weight.

The fish were kept in groups as pilot experiments indicated that small fish kept isolated refused to feed and either swam around agitatedly or did not move. In the experiments, exact statistical arrangement was sacrificed in favour of more ecologically and physiologically relevant results.

At the start and end of every experiment each fish was anesthetized, with MS 222 blotted on soft wet paper, and weighed to the nearest 0.01 g.

Live Chaoborus larvae served as food. They were concentrated in a cup with a net bottom and their wet weight was estimated to the nearest 0.01 g before they were fed to the fish. The overflow of the aquaria was supplied with a net to prevent the larvae from being washed out. The fish had continual access to live food.

### Growth rate

The fishes' growth rates were assumed to be exponential. Specific growth rates expressing daily percentage weight changes were calculated according to the formula:

$$G_w = \frac{\ln w_2 - \ln w_1}{t} \times 100$$

where  $G_w$  is the specific growth rate,  $w_2$  and  $w_1$  wet weight of the fish at the end and start of an experiment and  $t$  is the duration of the experiment in days.

### Food consumption

Total food consumption during an experiment was estimated by adding the weight of the food rations supplied and subtracting the amount of food left when the experiments were terminated. The wet weights of fish and food were transformed to organic dry weights before the consumption rates were calculated. For this transformation, organic dry weight values were calculated after drying to constant weight at 65 °C and subtracting the rest of ignition at 560 °C. Fish for this analysis were taken from the same lake, at the same time of year, as the experiment fish.

Food consumption rate (R) was estimated as daily mean ration on a percentage basis of fish weight according to the formula:

$$R = \frac{C}{t \times \frac{W_1 + W_2}{2}} \times 100$$

where  $C$  is the total food consumption in an experiment expressed in organic dry weight,  $t$  is duration of the experiment in days and  $W_1$  and  $W_2$  are organic dry weights of the fish at the start and end of the experiment.

### Food conversion

Food conversion efficiency (K) was estimated with organic dry weights according to the formula:

$$K = \frac{W_2 - W_1}{C} \times 100$$

where  $W_2$  and  $W_1$  are the weights of the fish at the end and start of an experiment and  $C$  is the total consumption during the experiment.



## Modelling data

To obtain models describing the relations between the independent parameter weight and the dependent parameters consumption rate, growth rate and food conversion at different temperatures, data were fitted to the following equations:

$$y = a + bx$$

$$y = ae^{bx}$$

$$y = a + b \ln x$$

$$y = ax^b$$

The best fit was chosen as model.

## RESULTS

### Growth

Preliminary analysis of the weight change data indicated that the growth rates were dependent on temperature and on the weight of the fish. I first attempted to find the relation between growth rate and fish weight for the different temperatures. The coefficient of determination ( $r^2$ ) indicated that, of the four tested models, the best general fit achieved by the regression was the equation:

$$G_w = a W^b \quad (1)$$

where  $G_w$  is the specific growth rate,  $W$  is the weight of the fish and  $a$  and  $b$  are constants whose values at the different temperatures are given in table 2.

The regression lines were extrapolated to the fish weight range 1-100 g (Fig. 1). The significance of the regression lines declined with temperature; weight contributed 95 % of the regression at 24 °C but less than 10 % at 4 °C (Tab. 2).

The growth rate decreased with increasing weight for all temperatures. The value of the weight exponent ( $b$ ) indicates the decline of growth rate with weight. A comparison of the regression lines for temperatures close to another, indicated that the weight exponent ( $b$ ) was significantly different for the temperatures 20 °C and 24 °C ( $p < 0.001$ , F-test) but not for the other temperatures ( $p > 0.05$ ). This means that at 24 °C the growth rate declined significantly faster with weight than at the other temperatures. The regression lines for 20 and 24 °C cut one another at a weight

of 30 g. Thus, for a 30 g perch, the growth rate was the same at 20 and 24 °C. For fish less than 30 g, the growth rate was higher at 24 than at 20 °C and for fish more than 30 g, the growth rate was lower at 24 than at 20 °C. In the temperature range 4-20 °C, the growth rate increased with temperature for all weights. At 28 °C the growth rates were estimated in only one experiment with four equal sized fish, so a regression could not be fitted in the same way as for the other temperatures. The fish had a mean weight of 3.2 g and the growth rates were extrapolated to be valid in the range 1-3.2 g in the following way. Assuming that the weight exponent  $b$  was the same at 28 and 24 °C for fishes weighing from 1-3.2 g, the constant  $a$  at 28 °C was calculated from the mean growth rates (11.1) and mean weight (3.2 g) of the four fish by substituting  $G_w$  and  $W$  in the equation (1).

The second step of modelling the data was to find the relation between growth rate and temperature for fixed weights. The growth rate values at different temperatures for 5 specific weights were calculated from equation (1), plotted, and the curves describing the growth rate temperature relation for the specific weights were fitted by eye (Fig. 2). Optimum temperature for growth varied with the weight of the fish and was higher for the smaller fish. It was assumed that the curves for different weights would reach maxima at specific temperatures and then decline. Curves were first drawn for the weights 30 and 100 g. For a 30 g fish, the growth rate was similar at 20 and 24 °C and I assumed that the maximum would be 22 °C. The maximum for a 100 g fish was reached at a lower temperature, while for 10 g, 3 g, and 1 g fish the maxima were higher - around 20-21 °C for a 100 g perch, 24 °C for a 10 g perch, above 28 °C for a 3 g perch and probably around 30 °C for a fish weighing 1 g.

#### Food consumption

Mean consumption rates were calculated for each of the different groups exposed to different temperatures and the relation between consumption and fish weight at the different temperatures was found. The coefficient of determination ( $r^2$ ), indicated that the best general fit achieved by the regression was the equation:

$$R = a + b \ln W \quad (2)$$

where  $a$  and  $b$  are constants whose values are given in table 3. Relative consumption increased with temperature and decreased with increasing weight (Fig. 3). The coefficient of determination decreased with decreasing temperatures in the range 24-8 °C.



The relation between relative consumption and temperature for the different weights was described using the equation (2) (Fig. 4). For fish in the range 1-100 g, the temperature for maximum consumption was above 24 °C, but the specific maximum temperature for different weights could not be estimated.

### Food conversion

The highest food conversion efficiency in all the experiments was recorded at 20 °C for a group of fish with a mean weight of 3.55 g (Fig. 5). At 24 and 20 °C food conversion declined with increasing weight. The best fit describing these relations was the equation:

$$K = a + b \ln W \quad (3)$$

where a and b are constants whose values are given in table 4. In the range 16-24 °C, food conversion efficiency was not dependent on weight and the mean values of conversion efficiency for all fish were calculated at the different temperatures. The relation between food conversion and temperature and weight was rather complex. Fish with a weight of less than 12 g were better food converters at 20 than at 16 °C, but this was reversed for fish bigger than this specific size. Food conversion was higher at 24 than at 16 °C for fish less than 3.5 g, and higher at 12 than at 24 °C for fish weighing more than 33 g. For all weights food conversion was better at 20 than at 24 °C. The temperature for optimum conversion changed with the weight of the perch and was approximately 20 °C for a 1 g fish, 17.5 °C for a 10 g fish and 16 °C for a 100 g fish (Fig. 6).

### Optimum temperature

The optimum temperatures for maximum food consumption, growth and food conversion were different for a specific weight. Highest optimum temperature was noted for food consumption and lowest for food conversion.

## DISCUSSION

### General aspects on accomplishment of the experiments

All fish were in good health throughout the experiments. They seemed to be well acclimatized to experimental conditions. No sign

of stress was observed and they fed vigorously. They started feeding within 15 minutes after they had been anesthetized, handled and weighed. Pilot experiments indicated that the water had to be renewed if the perch were to attain maximum growth rate and consumption. Fish kept in stagnant water stopped feeding after one day, or ate little, even when the oxygen content of the water was sustained by aerating. With continuous water renewal, no harmful effects were observed and the oxygen content never fell below 80 % saturation.

The high consumption and growth rates in my study were probably due to the fact that the fish could feed continuously and that the water was constantly renewed and cleaned of harmful waste products. Ammonia, even in low concentrations, might decrease food consumption and growth (Woltering et al 1978, Alderson 1979). It was necessary to keep small fish in groups as they refused to feed when isolated. However, bigger individuals did not show this tendency when isolated or kept in pairs. Jezierska (1975) did not find that keeping 20 g to 60 g perch isolated had a negative effect on consumption and growth. Estimating mean consumption over a period of several days results in a more reliable estimate than the short time feeding of starved fish which might result in higher consumption rates on the first day after starving.

#### Growth rate

I found that the model which best describes the correlation between the growth rate and weight of perch was that previously found to be the best simple fit for Salmo trutta (Elliott 1975). At a fixed temperature, the growth of my perch in my experiments decreased when the weight increased which is in accordance with the results obtained for the fish Oncorhynchus nerka (Brett and Shelbourn 1975), S. trutta (Elliott op cit) and Coregonus fera (Gunkel 1981) and for the crustacean, Gammarus pulex (Sutcliffe et al 1981).

The correlation between growth rate and weight was best at high temperatures. Since the growth rate was very low at 4 and 8.2 °C, even small individual deviations from the mean greatly decrease the significance of the correlation. As the growth rate of females generally exceeds that of males in natural conditions, part of the dispersion in growth rates may be due to sex. However, the effect of this factor was not taken up in this study.

The maximum growth rates in my study are much higher than those previously reported for perch of a similar size (Willemssen 1977), for yellow perch, Perca flavescens (Schneider 1973), S. trutta (Elliott 1975), O. nerka (Brett and Shelbourn 1975), C. fera (Gunkel 1981)



or for Lepomis macrochirus (Beitinger and Magnuson 1979). Schneider (1973) studied the influence of temperature on the growth of yellow perch. At the lowest temperature in his study, 11 °C, our results were in good agreement, but at higher temperatures Schneiders values are less than half of those obtained in my study. However, Schneider did not feed his fish continuously or on week ends, and he had troubles with acclimatization and the mortality rate was high. The time of the year and seasonal changes in growth hormones, may also have contributed to this discrepancy as his experiments were run in winter at high temperatures.

Schneider tested three kinds of foods but food-type did not seem to effect growth rates. The may fly larvae he used were probably most similar to the larvae used in my study. In Schneider's study, however, the highest growth rate was obtained on a fish diet. Feeding pattern is important for growth rate (Shelbourn et al 1973) and may be partly responsible for the differences between my results and those of Schneider (op cit) and Willemsen (op cit).

The growth rates for yellow perch in a simulated bioenergetic model (Kitchell et al 1977) contradicted my results. This model had no lag phase for growth at low temperatures and for a 10 g fish, the growth rate at 4 and 8 °C was about 1.5 % and 2 % per day, whereas the corresponding values in my study were 0.07 % and 0.17 % per day - more than a tenfold difference. At high temperatures, the growth rates differed as well. This indicates that P. fluviatilis and P. flavescens are differently temperature adapted. However, the model of Kitchell et al (op cit) was based on data from other fish species at low temperatures since data for perch were not available.

Since growth was much retarded and approached zero at temperatures below about 12 °C, it was almost irrelevant whether the temperature was 8 or 4 °C. On the other hand, when the temperature increased from 16 to 20 °C, the growth rate for a 3 g fish increased twofold.

### Consumption

The correlation between weight and relative food consumption was best at 20 and 24 °C. Less good correlation at 8 and 12 °C probably depended on the relatively low total consumption and the curve describing the consumption/temperature relationship had a lag phase in the range 4-12 °C. Relative differences between the consumption

rates for males and females may be greater, at lower temperatures than at high temperatures, and this may have contributed, but this was not investigated in my study.

Relative consumption decreased as the weight increased, in accordance with results from studies of other fish species such as Megalops cyprinoides, Ophiocephalus striatus (Pandian 1967), Limanda limanda (Pandian 1970), Onchorynchus nerka (Brett 1971), Salmo trutta (Elliott 1975), Phoxinus phoxinus, Gasterosteus aculeatus (Wotton et al 1980), Coregonus fera (Gunkel 1981) and the crustacean Gammarus pulex (Sutcliffe et al 1981).

I expressed consumption rates as organic dry weight values of both fish and food since these values are most comparable. Wet weight or dry weight values could not be used as the water and ash content differed in the food and in the fish. At a temperature of 24 °C, the daily food consumption would have been 78 % in wet weight units for a 1 g perch, 29 % in dry weight and 31 % in organic dry weight.

The perch in my study consumed about twice as much food as the fish in Schneider's (1973) and Willemssen's (1977) studies, probably for the same reasons that caused the differences in growth rates.

The discrepancy between Schneider's (op cit) and Willemssen's (op cit) studies and my experiments indicates that consumption and growth is higher when the fish are fed small food items like Chaoborus than when they are fed fish. Feeding on small food items is more continuous, the stomach is kept filled and digestion is more intense. Whereas, if the fish are fed big prey such as fish, additional food is not consumed until enough food has been digested and evacuated from the stomach to make room for the next big prey item.

#### Food consumption in field experiments

In field estimates by Nukashima and Leggett (1978), the maximum daily ration for perch ranging from 83-200 mm was 6.7 %. Nukashima and Leggett reviewed other studies and concluded that the daily ration varied from zero to less than 7 %, which is less than what even the biggest fish in my study consumed.

Also for smaller perch food limitation is often severe. Young (0+) perch consumed food corresponding to 7-28 % of their body weight per day (Spanovskaya and Grygorash 1977). These fish consumed less food than bigger fish in my experiments. In Oneida Lake, at temperatures close to 20 °C, the daily ration based on energy values averaged 21 % of the body weight of fish weighing less than 1 g (Mills and Forney 1981).

Comparing my estimattions of maximum food consumption to field studies, indicate a limited food supply under natural conditions

#### Optimum temperature

The fact that the optimum temperature for growth of perch is different for different weights explains the discrepancy between the optimum temperatures for growth estimated in other studies. For a 0.5 g yellow perch, 28 °C was the optimum temperature (McCormick 1976, qouted by Hokanson 1977), 23 °C for 5.2-23.7 g yellow perch (Schneider 1973) and 26 °C for 33-72 g perch (Willemssen 1977). It has previously pointed out that bigger individuals of some species have lower optimum temperatures than smaller individuals (Pandian 1970, McCauley 1977, Kitchell 1979).

If I had done experiments up to the lethal temperatures for perch, it would have been possible to estimate optimum temperatures for food consumption and growth for perch of all sizes. However, the aim of this study was primarily to obtain data on perch which would be useful in the evaluation of the effects of temperature on the ecology of perch in Swedish waters, where temperature seldom exceeds 24 °C.

#### Ecological effects of the different temperature optima for different weights of perch

If temperature is to be regarded as an ecological resource (Magnuson et al 1979), it may be treated as a niche dimension. That different sized perch have different optimum temperatures or are differently adapted to different temperatures, means that niche separation can take place along the temperature axis and thus reduce intraspecific interactions. In this way, the temperature factor would increase the habitat diversity and the total niche of perch. This would be advantageous and result in a greater abundance than if all individuals of a species were adapted to the same temperature.



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Table 1. Experimental conditions for the study of maximum food consumption, maximum growth rate and food conversion of perch at various temperatures.

| Temperature<br>°C | Time of year | Diurnal regime<br>light/dark<br>hours | Duration<br>time<br>days | Starving<br>prior to<br>weighing<br>hours | Size of<br>fish<br>g | Number of<br>fish |
|-------------------|--------------|---------------------------------------|--------------------------|-------------------------------------------|----------------------|-------------------|
| 28                | Sept.        | 18/6                                  | 7                        | 12                                        | 2.3-3.6              | 4                 |
| 24                | Sept.        | 18/6                                  | 8                        | 12                                        | 2.0-77.7             | 20                |
| 20                | Oct.         | 18/6                                  | 11                       | 12                                        | 3.0-44.8             | 16                |
| 16                | Nov.         | 18/6                                  | 14                       | 18                                        | 4.6-58.1             | 16                |
| 12.2              | Nov.Dec.     | 18/6                                  | 20                       | 24                                        | 3.5-70.7             | 17                |
| 8.2               | Dec.Jan.     | 12/12                                 | 25                       | 36                                        | 4.0-78.1             | 17                |
| 4                 | Jan.Mar.     | 12/12                                 | 35                       | 36                                        | 4.2-82.2             | 17                |

Table 2. Values of the coefficient of determination ( $r^2$ ) and the constants a and b in the growth rate equation  $G = a W^b$ , describing the relation between specific growth rate ( $G_w$ ) and weight of perch (W) at different temperatures. The F-test was used to test the significance of the regressions.

| T, °C | a      | b $\pm$ 95 % CL  | $r^2$ | p     |
|-------|--------|------------------|-------|-------|
| 24.0  | 15.300 | -.403 $\pm$ .048 | .95   | <.001 |
| 20.0  | 8.973  | -.252 $\pm$ .052 | .89   | <.001 |
| 16.0  | 4.107  | -.200 $\pm$ .120 | .48   | <.005 |
| 12.2  | 1.689  | -.445 $\pm$ .317 | .37   | <.01  |
| 8.2   | 0.363  | -.335 $\pm$ .328 | .24   | <.05  |
| 4.0   | 0.101  | -.157 $\pm$ .338 | .07   | <.50  |

Table 3 Values of the coefficient of determination ( $r^2$ ) and the constants a and b in the consumption rate equation  $R = a + b \ln W$ , describing the relation between daily food consumption (R) expressed as a percentage value of fish weight (W) at different temperatures (T).

| T, °C | a     | b      | $r^2$ |
|-------|-------|--------|-------|
| 24.0  | 31.46 | - 4.61 | .95   |
| 20.0  | 17.68 | - 1.81 | .99   |
| 16.0  | 11.50 | - 1.68 | .84   |
| 12.2  | 4.59  | - 0.74 | .40   |
| 8.2   | 2.80  | - 0.36 | .31   |
| 4.0   | 1.43  | - 0.21 | .88   |

Table 4. Values of the coefficient of determination ( $r^2$ ) and the constants a and b in the food conversion equation  $K = a + b \ln W$ , describing the relation between food conversion efficiency (K) and fish weight (W) at 20 and 24 °C. Mean values of food conversion efficiency ( $\pm$  95 % C.L.) for all fish are given at other temperatures.

| T, °C                           | a                | b     | $r^2$ |
|---------------------------------|------------------|-------|-------|
| 24.0                            | 40.72            | -4.67 | .81   |
| 20.0                            | 47.09            | -4.80 | .97   |
| Food conversion $\pm$ 95 % C.L. |                  |       |       |
| 16.0                            | 34.66 $\pm$ 3.26 |       |       |
| 12.2                            | 25.51 $\pm$ 3.82 |       |       |
| 8.2                             | 10.12 $\pm$ 3.09 |       |       |
| 4.0                             | 8.44 $\pm$ 5.15  |       |       |

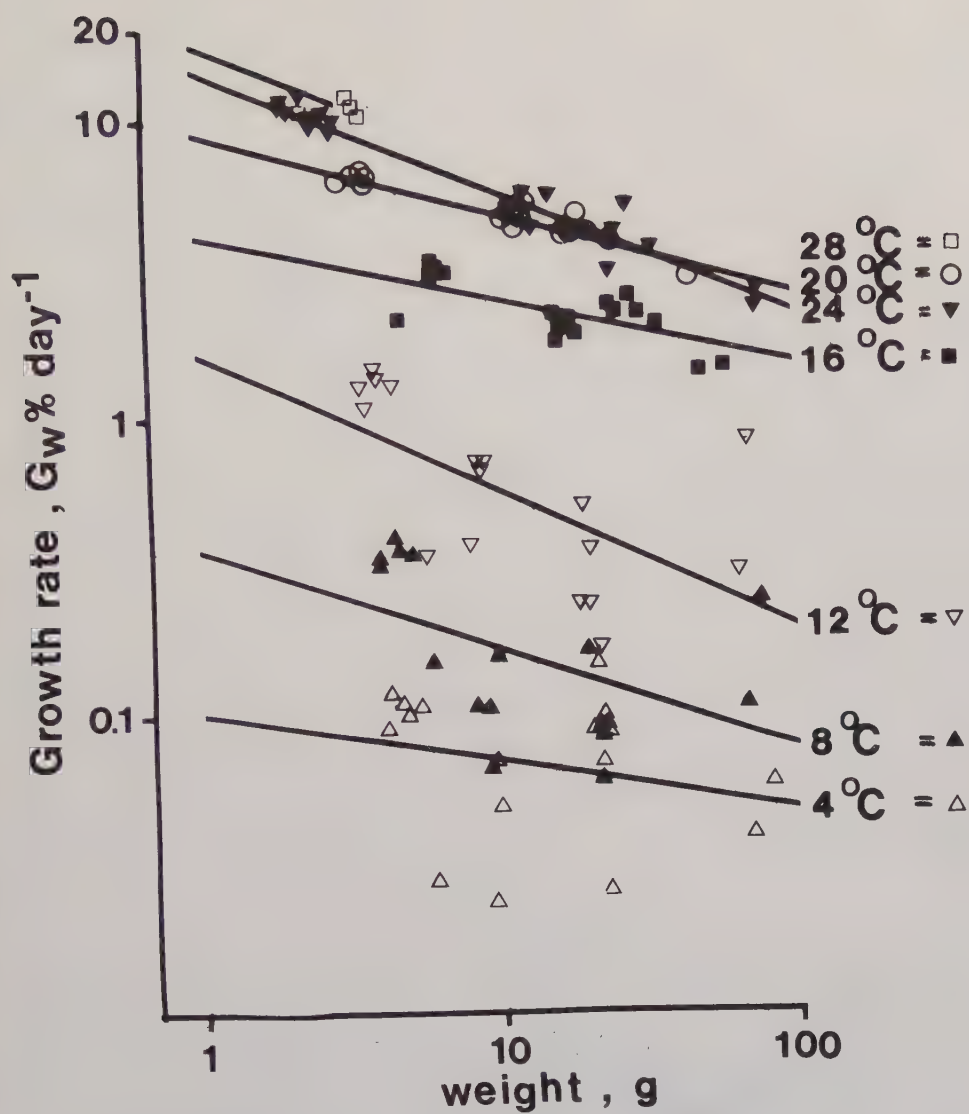


Fig. 1. Relationship between growth rate and mean weight of perch at different temperatures.



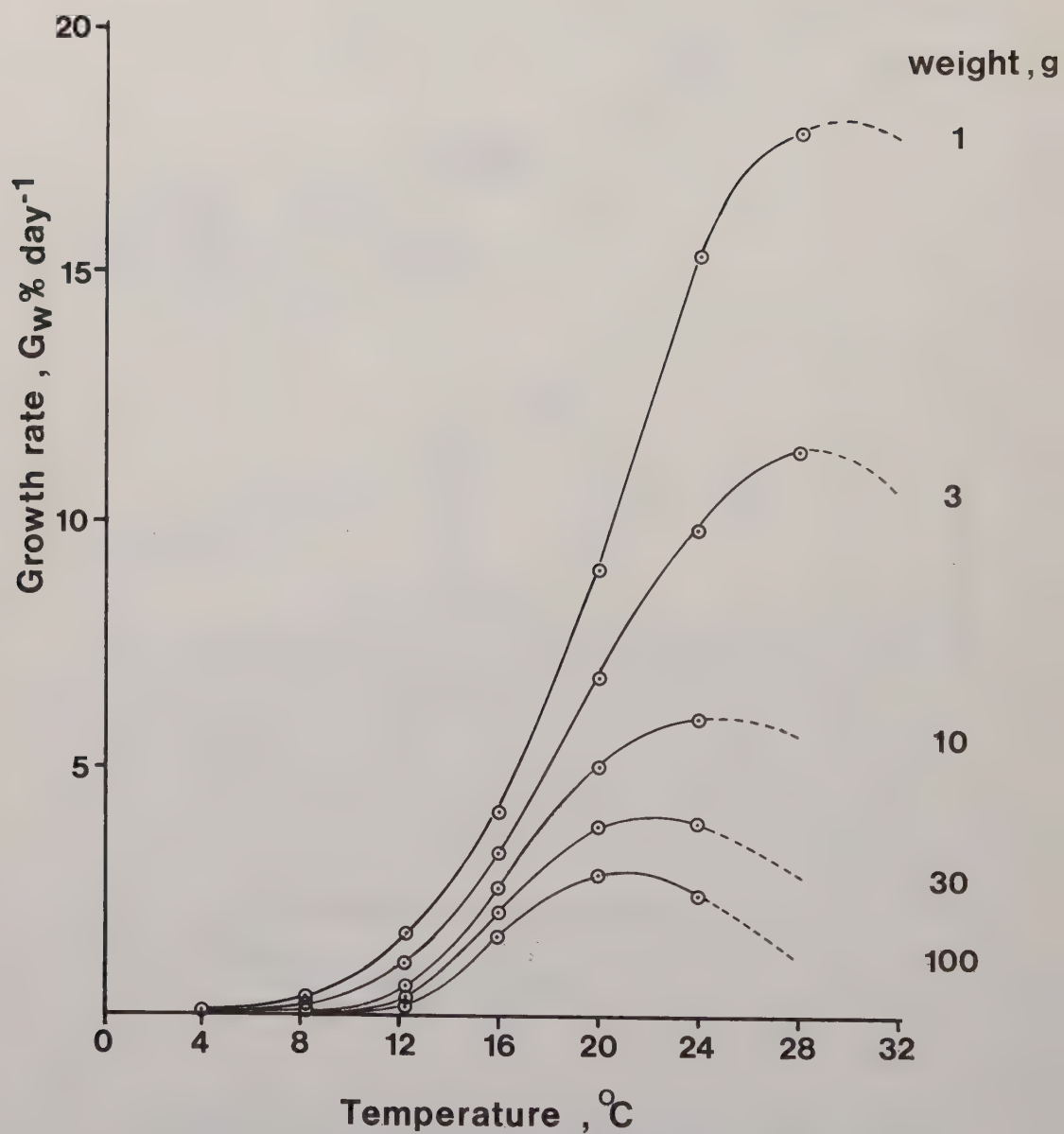


Fig. 2. Relationship between calculated growth rate and temperature for different weights of perch.

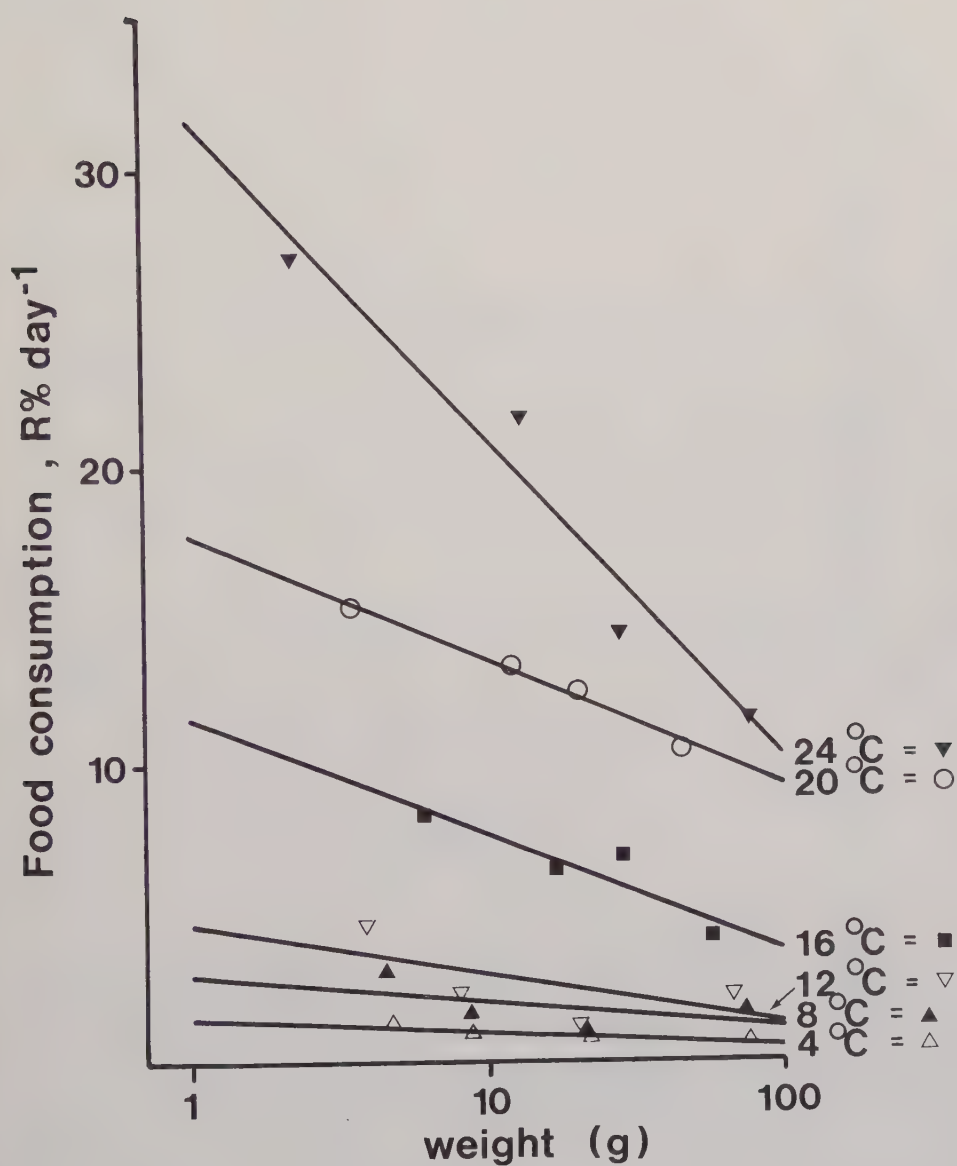


Fig. 3. Relationship between mean food consumption and mean weight of perch at different temperatures.

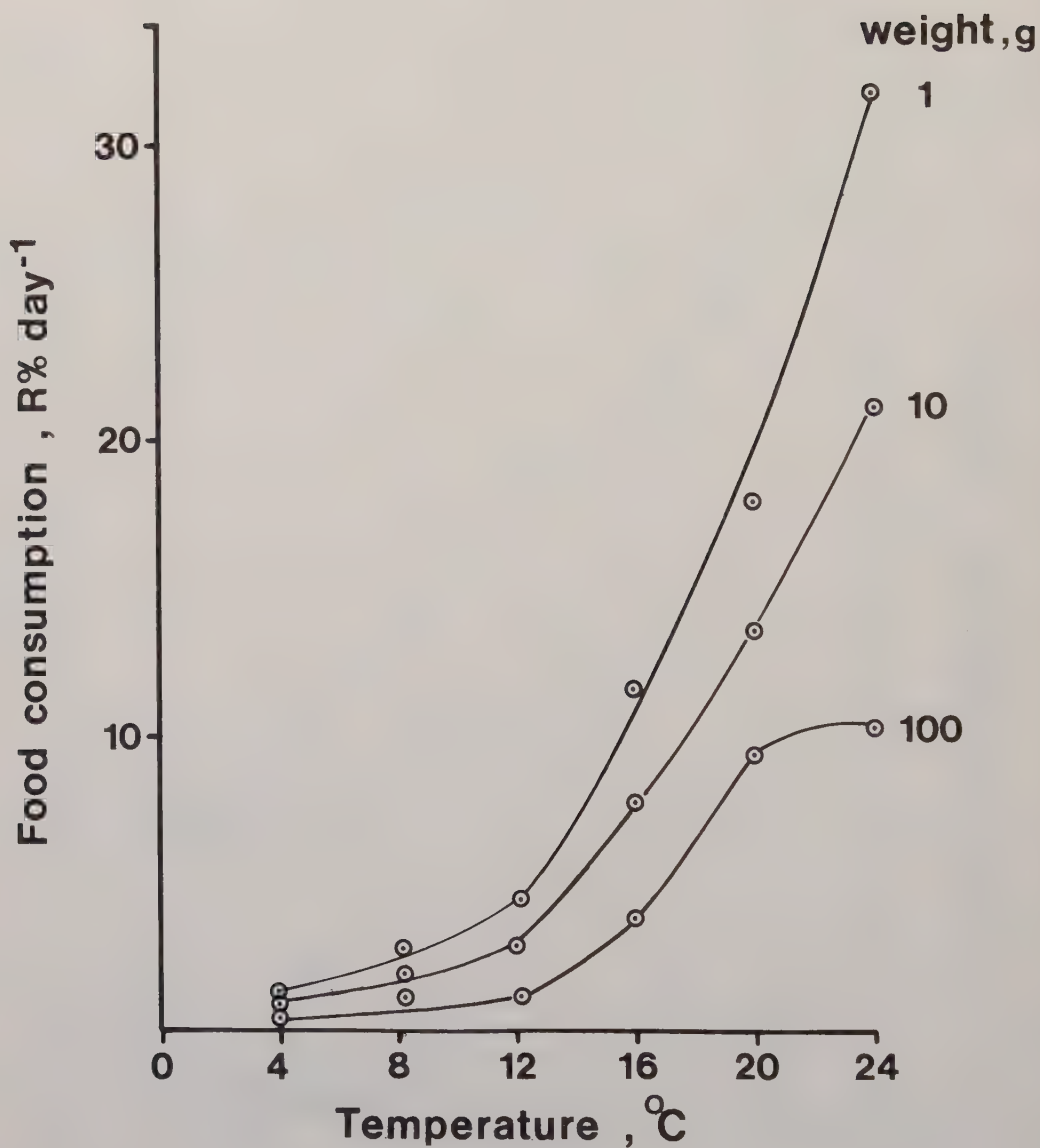


Fig. 4. Relationship between calculated food consumption and temperature for different weights of perch.



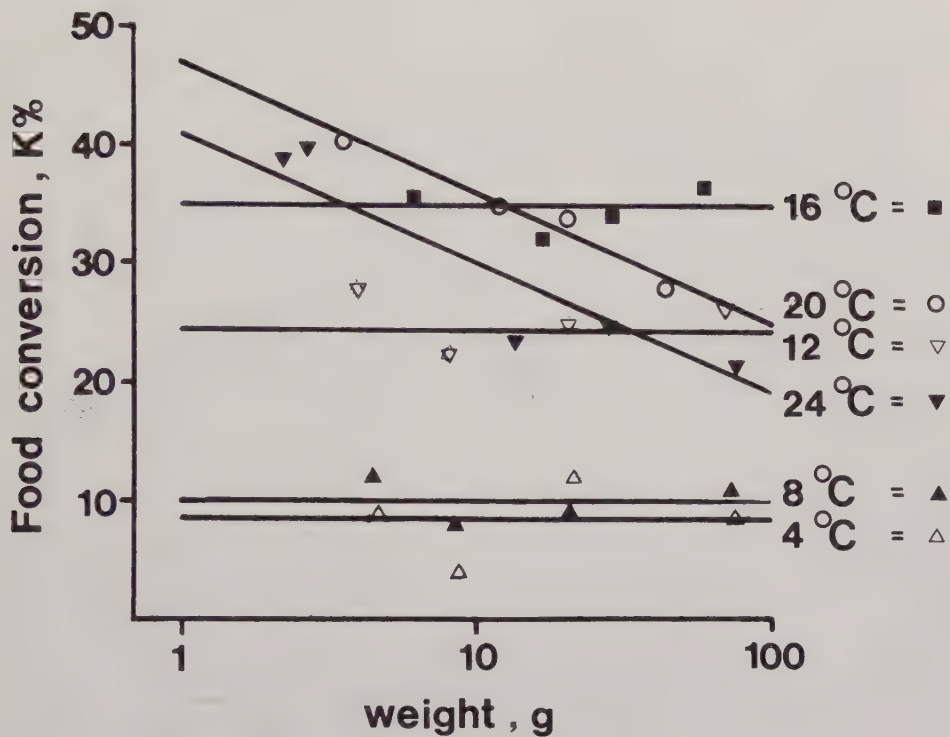


Fig. 5. Relationship between food conversion efficiency and weight of perch at different temperatures. At 4-16 °C the lines describe mean values for fish of different weights. At 20 and 24 °C the lines are regression lines for the best fit.

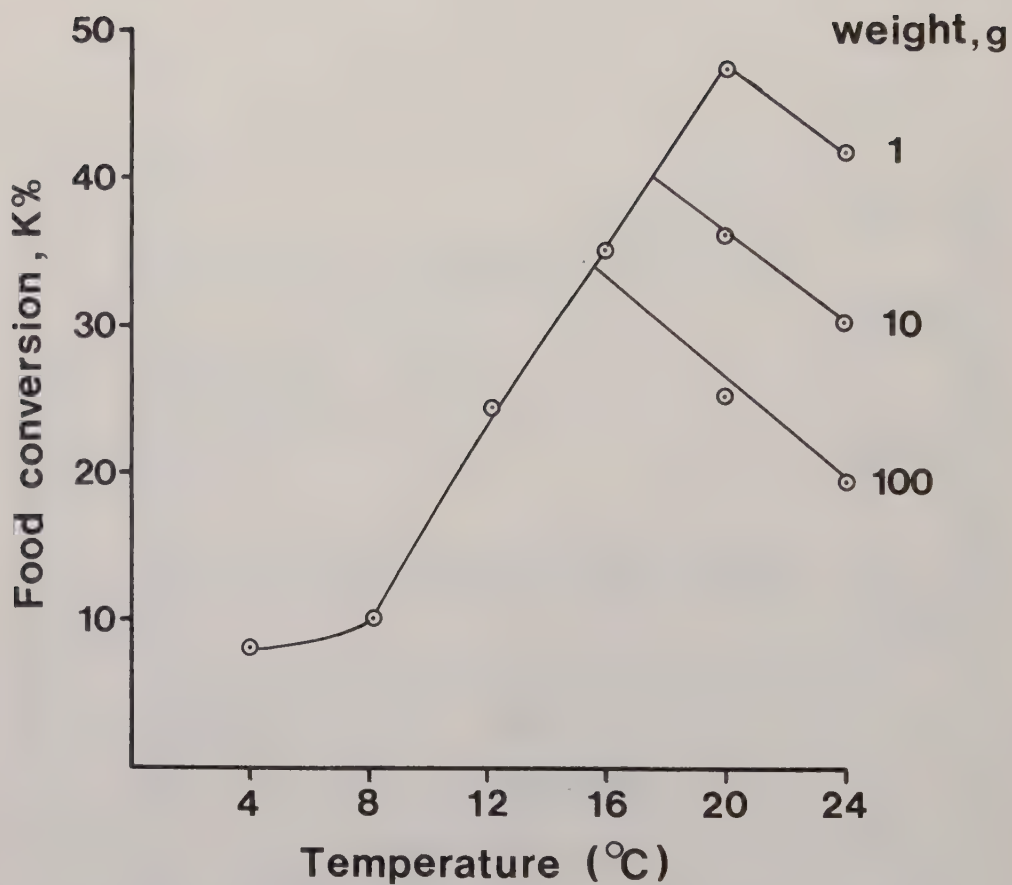


Fig. 6. Relationship between calculated food conversion efficiency and temperature for different weights of perch.

EFFECTS OF RATION SIZE AND TEMPERATURE ON GROWTH  
AND FOOD CONVERSION OF PERCH (*Perca fluviatilis*).

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## SUMMARY

The effect of ration size on the growth and food conversion of perch (Perca fluviatilis) weighing close to 2 g, was studied at the temperatures 4, 8, 12, 16, 20 and 24 °C. Growth rate increased almost lineally to ration in the temperature range 12-24 °C. Temperature and ration size influenced growth and food conversion in a complex way. Maximum values for food conversion (approx. 40 %) were attained at about 20 °C.

## INTRODUCTION

The growth and food conversion of perch (Perca fluviatilis) and yellow perch (P. flavescens) at different ration sizes and temperatures was studied by Solomon and Brafield (1972), Schneider (1973), Jezierska (1975) and Willemsen (1977). The total temperature and ration range relevant to perch has not been studied, as previously have been done for other fish species, such as Onchorynchus nerka (Brett et al.1969) and Salmo trutta (Elliott 1976).

In a previous work on the energetics of perch, it was shown how growth rate, food consumption and food conversion were influenced by temperature and by the weight of fish fed maximum rations (Lessmark 1983a). The purpose of this work is to estimate the influence of ration size and temperature on the growth rate and food conversion of perch, over the wide range of ration and temperatures occurring in natural conditions.

## METHODS

Fish weighing about 2 g (range 1.2-3.9 g) were kept in 60 litre aquaria with a continuous through-flow of fresh water. A group of generally five fish were kept in each aquarium at temperatures of 4, 8, 12, 16, 20 and 24 °C. Temperatures were co-ordinated with seasonal changes in temperature in the natural environment. The groups of fish were fed varying amounts of food. Details are presented in table 1.

After acclimatization to experimental conditions, each group of perch was fed a defined daily ration of live animal food for a varying number of days. A diet of Daphnia magna was used for all temperatures except for 4 °C, when Chaoborus was used instead. At 24, 20 and 16 °C, the daily ration consisted of four equal sized meals

spread over a 12 h period. At 12 and 8 °C, two meals were given daily and at 4 °C, one meal. Prior to the start and termination of an experiment the fish were starved to evacuate the gut.

Replicate experiments were run in two years at temperatures ranging from 12 to 24 °C. To study how season effect growth and food conversion, the experiments were run at different times of the year (Tab. 1).

The experimental set up and realization, handling and weighing of fish and food animals and calculations of specific growth rate and food conversion were the same as those previously described by Lessmark (1983a). Data from this previous study on growth and food conversion for fish on maximum rations has been used in this paper.

Growth rates were calculated as specific growth rates and expressed as percentage weight-increase per day ( $G_w \text{ \% day}^{-1}$ ). Food consumption was related to body weight and expressed as a percentage of fish weight per day ( $R \text{ \% day}^{-1}$ ). Food conversion efficiency was calculated on a percentage basis and expressed as weight-increase per amount of consumed food ( $K \text{ \%}$ ).  $R$  and  $K$  were estimated on organic dry weight values.

## RESULTS

### Effects of ration size and temperature

Growth rate increased with ration size at all temperatures and the curves describing these relationships were fitted by eye (Fig. 1). At rations above maintenance, i.e. the ration that covers metabolic demand and growth rate is zero, straight lines would also have been good approximations for these relations in the temperature range 12 to 24 °C. Replicate experiments performed in different years were in good agreement.

Food ration and temperature interacted and effected growth rates (Fig. 2). At maximum rations, the optimum temperature for growth was above 24 °C. As rations decreased, the optimum temperature tended to be lower e.g. the optimum temperature for growth at a ration of 2 % was 12 °C and at a ration of 15 %, it was 20 °C. There were exceptions, however, and in a broad ration range, the growth rate was higher at about 20 °C than at other temperatures.

Maintenance ration increased with increasing temperature from about 0.6 % at 4 °C to 4 % at 24 °C (Fig. 1).

Food conversion efficiency increased with increasing ration at 20 °C (Fig. 3). At 12, 16 and 24 °C it increased to a plateau value

for a certain ration and maintained this level even when the ration increased. Both temperature and ration influenced food conversion, which attained maximum value at about 20 °C (Fig. 4 and 5). Since food conversion attained maximum value at 20 °C, perch weighing about 2 g were best adapted physiologically, to utilize food at this temperature.

#### Effect of season

Season did not influence growth rates. At 12 °C, the results were the same, regardless of wheather experiments were run in May or in December (Fig. 1). At other temperatures there was also good agreement between the results at different times of the year.

#### DISCUSSION

The curves describing the relationship between ration size and growth rate were probably partly determined by the behaviour of the perch. In the temperature range 16 to 24 °C, fish fed rations close to maintainance ration swam more agitatedly than fish fed rations closer to the maximum ration. This was probably food searching behaviour induced by hunger, which increased metabolic demands to the detriment of growth.

At 4 and 8 °C, the disparity in growth rates was relatively large, due to small weight changes and low growth rates (Fig. 1). Under these conditions, the values are less exact than at higher temperatures. However, this is not very significant in ecological terms because growth is slow at low temperatures.

Growth rate and food conversion was higher at 20 than at 16 °C in a broad ration range. This contradicts the results from experiments on other fish (Brett et al. 1969, Elliott 1976, Medvick 1979), which state that lower temperatures become more favourable for growth, when food rations are less, due to the fact that respiratory costs decrease with decreasing temperature. However, it has been found that optimum temperature is independent of ration. Andrews and Stickney (1972) achieved best conversion for Ichthalurus punctatus at 30 °C, independent of wheather the daily ration was 2, 4 or 6 % of the weight of the fish. Also, for Carassius auratus growth was faster on equal rations at 20 than at 16 °C (Davies and Massey 1977), and this is in agreement with my results. When perch were fed maximum rations, food conversion was dependent on tempera-

ture (Lessmark 1983a) and attained maximum values at different temperatures, depending on the weight of the fish. For fish weighing less than 13 g, the optimum temperature for food conversion was about 20 °C (Lessmark op cit), as in this study. On equal rations, growth rate and food conversion were higher at 20 than at 16 or 24 °C. This must depend on the following: (1) either that assimilation is most efficient at 20 °C, or (2) that energy requirements for "apparent specific dynamic action" (Beamish 1974, quoted by Elliott 1979) (including costs for absorption, digestion, deamination, movement and deposition of food and other conversion processes) are lowest at 20 °C, or (3) a combination of these factors. This would explain why growth was faster at 20 °C than at 16 and 24 °C on equal rations, and why conversion attained maximum value at 20 °C.

As in previous studies on perch and yellow perch ( Willemsen 1977, Schneider 1973), there was almost a direct linear relation between growth rate and ration. High rations resulted in a decline in the growth rate of salmonids (Warren and Davies 1967, Brett et al. 1969, Elliott 1976, Wurtsbaugh and Davis 1977) i.e. at a certain temperature, food conversion was higher and reached maximum value below maximum ration. The curves describing these relations have frequently been assumed valid even for other fish, but they are not valid for perch.

The food conversion efficiency of young yellow perch, fed Daphnia pulex was indirectly estimated to be in the range 11-38 % at temperatures between 18 and 20 °C (Mills and Forney 1981). Winberg (1956) calculated that, theoretically, conversion efficiency would never attain values above 50 %. Compared to other studies on conversion efficiency in fish, the values attained in my study are among the highest ever recorded.



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Table 1. Experimental conditions for studying growth rate and food conversion of perch fed varying ration-sizes at various temperatures.

| Temperature<br>°C | Time of year    | Duration of<br>experiments<br>days | Number of<br>experiments |
|-------------------|-----------------|------------------------------------|--------------------------|
| 4                 | Feb.-Mar.       | 20                                 | 4                        |
| 8                 | Apr.-May        | 17                                 | 3                        |
| 12                | May, Dec.       | 14-27                              | 4                        |
| 16                | Oct.,Nov.       | 14                                 | 4                        |
| 20                | Jul.,Sept.,Nov. | 9-10                               | 7                        |
| 24                | Jul.,Aug.-Sept. | 9                                  | 4                        |

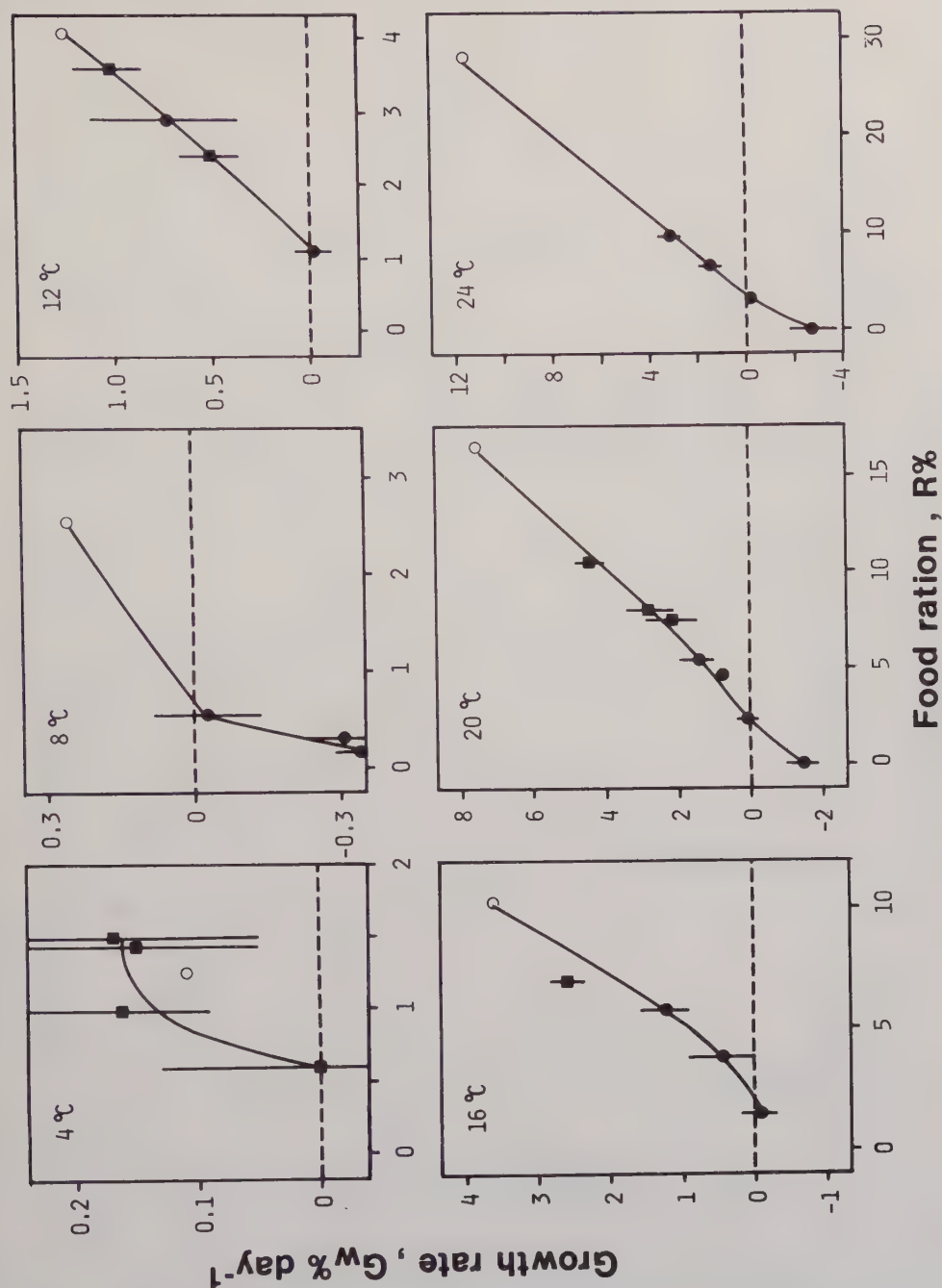


Fig. 1. Relationship between growth rate,  $\pm$  95 % C.L. and ration-size at different temperatures for perch weighing about 2 g. Solid circles and squares represent results from different years. Empty circles represent results on maximum rations of the dipteran larvae Chaoborus (Lessmark 1983a).



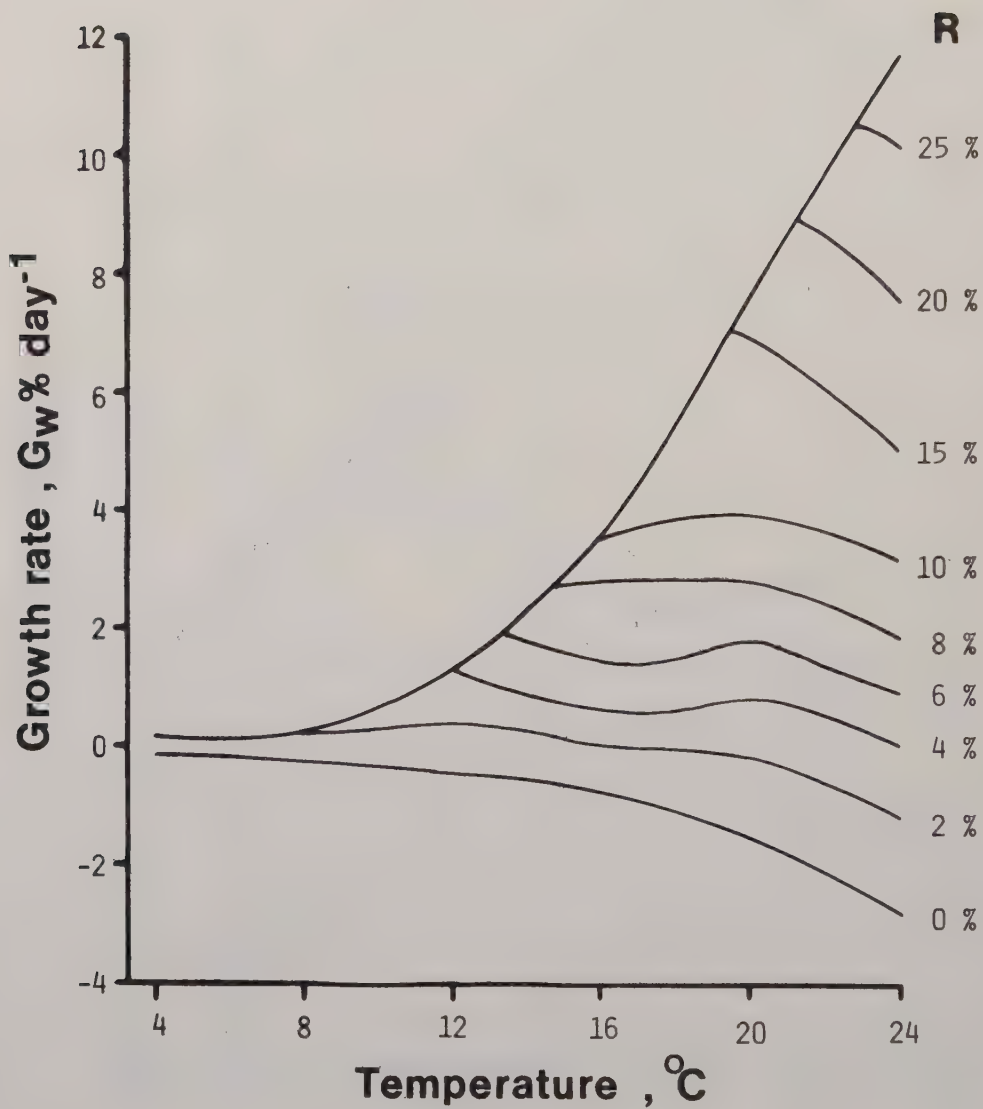


Fig. 2. Growth rate of perch at different temperatures and ration-sizes (R). Curves were fitted from the data in figure 1.

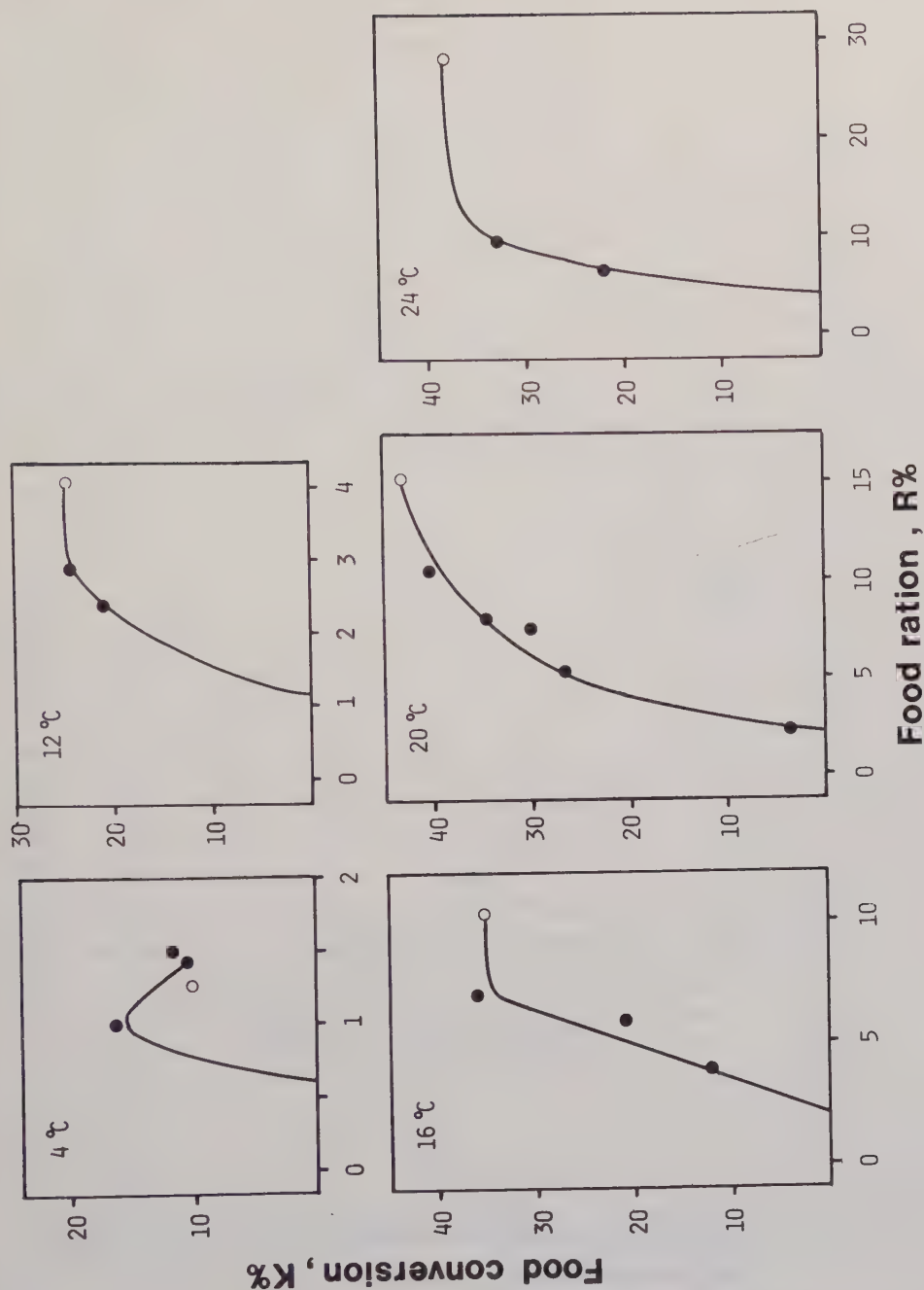


Fig. 3. Relationship between food conversion efficiency and ration-size at different temperatures for perch. Solid circles indicate results on a diet of *Daphnia* (at 4 °C *Chaoborus*) and empty circles represent results on maximum rations of *Chaoborus* (Lessmark 1983a). Note the different scales on the axes.

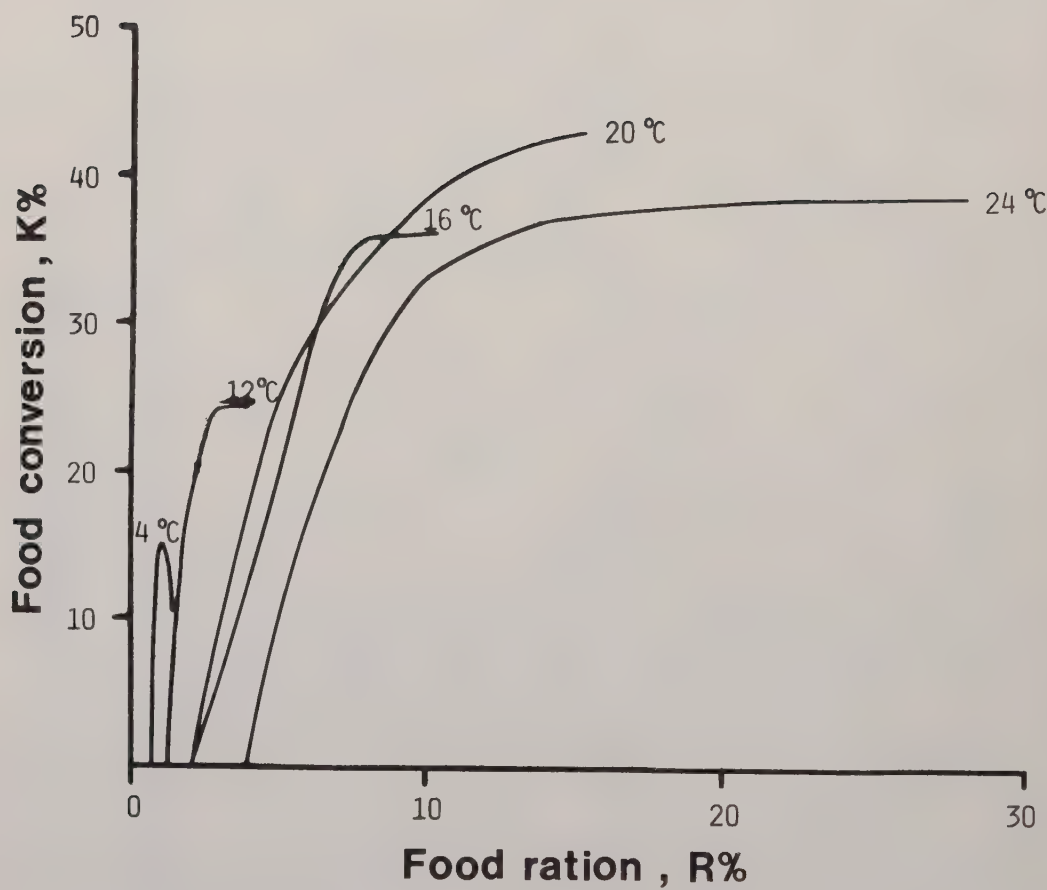


Fig. 4. Food conversion in perch for varying ration-sizes and at different temperatures.

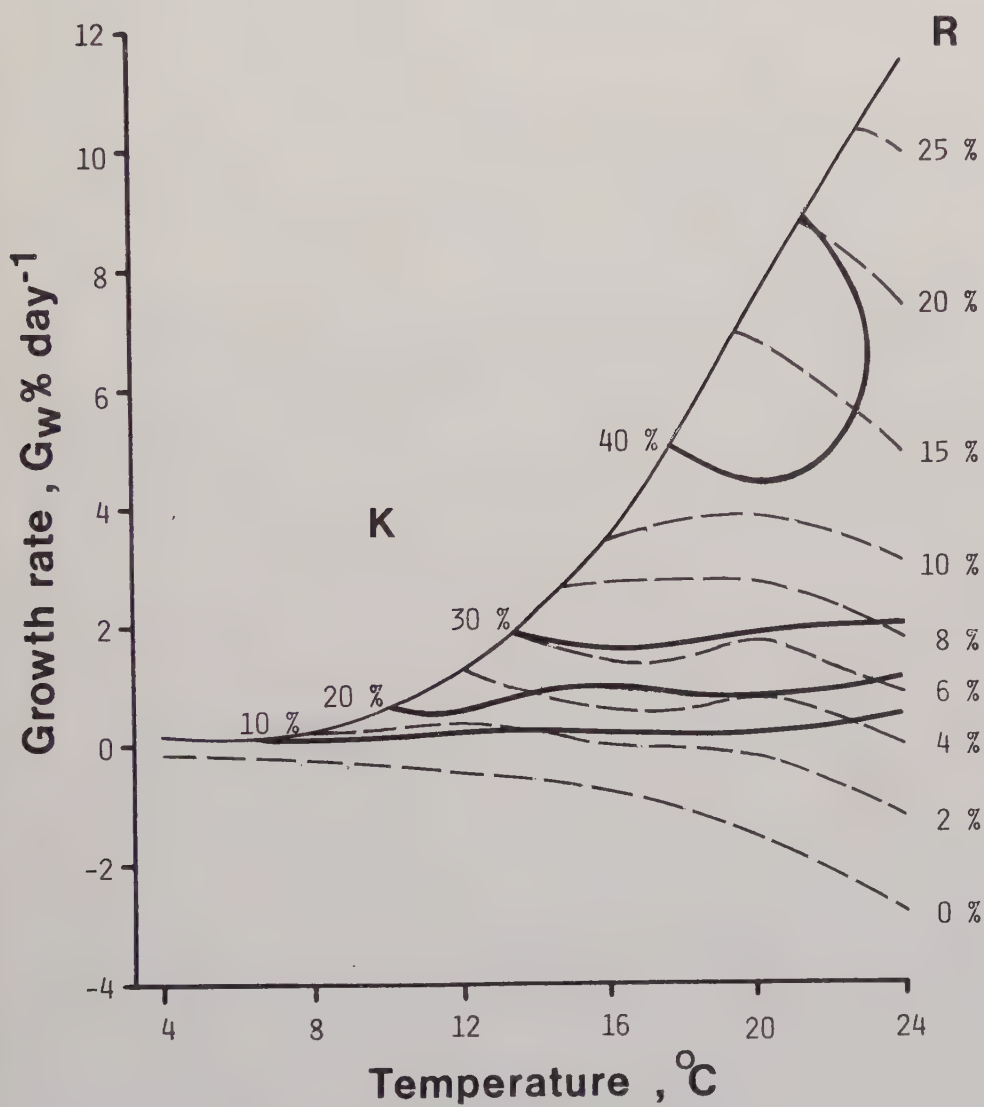


Fig. 5. Isopleths for food conversion (K) in perch for varying ration-sizes (R) and at various temperatures.





EFFECTS OF TEMPERATURE AND WEIGHT ON FOOD CONSUMPTION,  
FOOD CONVERSION AND GROWTH OF ROACH (*Rutilus rutilus*)  
FED MAXIMUM RATIIONS

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## SUMMARY

In laboratory experiments, roach (Rutilus rutilus) weighing between 1 and 50 g were fed maximum rations of live Chaoborus larvae at temperatures of 4.0, 8.2, 12.2, 16, 20 and 24 °C. Food consumption and growth rate increased with temperature and was independent of the weight of the fish over the range of temperatures between 4 and 20 °C, but declined with increasing weight of the fish at 24 °C. The temperature at which maximum food consumption and growth occurred declined with increasing weight of the fish. The optimum temperature for growth was about 20-24 °C for 50 g fish but was higher than the studied temperature range for smaller fish. Food conversion was most efficient at 20 °C for all weights. For a 10 g fish, maximum daily food consumption was 24 % of weight (organic dry weight), daily growth rate 3.8 % at 24 °C and maximum food conversion 23 % at 20 °C.

## INTRODUCTION

Temperature contributes to the success of a species in its environment and as such is an important factor in the regulation and structuring of fish populations (Lessmark 1983e with references). However, little research has been done on the effect of temperature on the consumption, growth rate and food conversion of European fish species. In the absence of more exact data on temperature optima, fish have been generally classified as cold or warm water species.

Field studies have generally concentrated on the amount of food an organism consumes, with little attention being paid to the quality of food, and to what degree the food is assimilated and converted into biomass. In an other work I estimated the utilization of plant food for growth by roach (Lessmark 1983f).

The aim of this study is to estimate the influence of temperature and weight on the food consumption, food conversion and growth of roach fed maximum rations of animal food. This was previously studied for perch, Perca fluviatilis (Lessmark 1983a).

## METHODS

The methods and calculations used were the same as those previously described by Lessmark (1983a) and here only shortly present-

ted. The fish were kept at constant temperatures and were fed live Chaoborus larvae. Growth rates were calculated as specific growth rates and expressed as percentage weight increase per day ( $G_w \% \text{ day}^{-1}$ ). Food consumption was related to body weight and expressed as a percentage proportion of fish weight per day ( $R \% \text{ day}^{-1}$ ). Food conversion efficiency was calculated on a percentage basis and expressed as weight increase per amount of consumed food ( $K \%$ ).  $R$  and  $K$  were estimated from organic dry weight values. A summary of experimental design are given in table 1.

## RESULTS

### Growth rate

At 24 °C, growth rate was dependent on weight, decreasing with increasing weight (Fig.1); the coefficient of determination ( $r^2 = 0.90$ ,  $p < 0.001$  F-test) indicated that the relationship was best described by the equation:

$$G_w = 7.50 W^{-0.2950} \quad (1)$$

where  $G_w$  is specific growth rate and  $W$  is fish-weight. Growth rate was not dependent on fish-weight for temperatures between 4 and 20 °C (Tab. 2, Fig. 1). Growth rate was lowest at 8 °C but increased with increasing temperatures.

For a 50 g roach, growth rate was about the same at 20 and 24 °C. I therefore assumed that optimal growth temperature for a 50 g roach was between 20 and 24 °C. For fish smaller than 50 g, growth rate was faster at 24 than 20 °C. Thus, temperatures for optimum growth varied according to fish size.

Growth rate values for specific weights and temperatures were calculated from table 1 and equation (1). These values were plotted, and the curves describing the relationship between growth rate and temperature for specific weights were fitted by eye (Fig. 2).

### Consumption

Relative daily consumption increased with increasing temperature. At 24 °C, but not at other temperatures, fish-weight effected relative daily consumption (Fig. 3). Mean consumption was calculated for the different groups of fish in the temperature range 4-20 °C (Tab. 2). At 24 °C the relationship between consumption and weight were best described by the equation:



$$R = 31.23 - 3.02 \ln W \quad (r^2 = 0.70)$$

where R is the daily, mean consumption expressed as percentage proportion of fish weight, and W is mean fish-weight.

Values describing the relationship between consumption and temperature for specific weight were calculated and the curves fitted by eye (Fig. 4) in the same way as the curves for the relationship between growth and temperature. Temperature for maximum consumption was higher than 24 °C for all weights tested, but it was obvious that the temperature for maximum consumption decreased as the weight increased.

### Food conversion

Food conversion efficiency was dependent on temperature and increased in the temperature range 12-20 °C (Fig. 5). Food conversion was weight-independent in that temperature range. Mean conversion efficiency for different weight groups was calculated (Tab. 2). At 24 °C, food conversion efficiency was dependent on fish-weight and conversion was more efficient for small individuals. The relationship between food conversion and fish-weight at 24 °C was best described by the equation:

$$K = 22.27 - 2.71 \ln W \quad (3)$$

where K is food conversion efficiency and W is mean fish-weight in grams.

Conversion efficiency was highest at 20 °C for all weights. For roach weighing less than about 2.5 g, conversion efficiency was higher at 24 than at 16 °C, and for heavier fish, food conversion was higher at 16 than at 24 °C.

Curves describing the relationship between food conversion and temperature for specific fish-weights were fitted by eye (Fig. 6) in the same way as the curves describing the relationship between growth and temperature.

### Optimum temperature

Temperatures for maximum growth, consumption and food conversion cannot be estimated exactly for any weight. Some conclusions can, however, be drawn. Food conversion for a 50 g roach was most efficient at about 20 °C, growth maxima were reached in the range 20-24 °C, and consumption maxima were reached above 24 °C. It follows,

therefore, that the optimum temperatures for these three metabolic functions increased in the order food conversion, growth rate and food consumption.

## DISCUSSION

Growth rate and relative food consumption generally decrease with decreasing fish-weight (Lessmark 1983a with references), which I also found for roach at 24 °C. However, at lower temperatures the weight of roach did not effect growth rate and food consumption. Up to about 20 °C, growth rate and consumption was the same for roach with different weights, but at higher temperatures different sized fish had different optimum temperatures. The largest fish probably approached the optimum for growth at about 20 °C, but for smaller fish the temperature optimum was even higher. This agrees for other studies on different fish species (Lessmark 1983a with references).

Growth rate was somewhat higher at 4 than at 8 °C, but this difference was small, and probably due to the fact that growth was insignificant at these temperatures.

The values for food conversion efficiency in roach were much lower than those recorded for perch (Lessmark 1983a) under similar conditions. As roach lack the protein splitting enzyme, pepsin (Kapoor et al. 1975), digestion and assimilation of protein-rich animal food is probably less efficiently. Roach, and many other cyprinids, feed to a great extent on plant material, which has high carbohydrate-content. Their digestive system is therefore adapted to use both plant and animal food. A disadvantage in this might be that they probably not assimilate high-protein animal food as efficiently as carnivorous fish like perch and salmonids.

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Table 1. Experimental conditions for the study of maximum food consumption, maximum growth rate and food conversion of roach at various temperatures.

| Temperature<br>°C | Time of year | Diurnal regime<br>light/dark<br>hours | Duration<br>time<br>days | Starving<br>prior to<br>weighing<br>hours | Size of<br>fish<br>g | Number of<br>fish |
|-------------------|--------------|---------------------------------------|--------------------------|-------------------------------------------|----------------------|-------------------|
| 24                | Sept         | 18/6                                  | 8                        | 12                                        | 1.6-46.4             | 17                |
| 20                | Oct          | 18/6                                  | 11                       | 12                                        | 2.3-13.8             | 14                |
| 16                | Nov          | 18/6                                  | 14                       | 18                                        | 2.9-24.6             | 18                |
| 12.2              | Nov-Dec      | 18/6                                  | 20                       | 24                                        | 3.4-32.0             | 19                |
| 8.2               | Dec-Jan      | 12/12                                 | 25                       | 36                                        | 3.5-31.9             | 18                |
| 4                 | Jan-Mar      | 12/12                                 | 35                       | 36                                        | 3.5-31.4             | 16                |

Table 2. Mean values ( $\pm$  95% C.L.) of growth rate, food consumption and food conversion efficiency of roach at different temperatures.

Temperature    Growth rate    Consumption    Food conversion

| °C   | $G_w$ % day <sup>-1</sup> | R %              | K %              |
|------|---------------------------|------------------|------------------|
| 20   | 2.494 $\pm$ .254          | 10.88 $\pm$ 4.17 | 22.73 $\pm$ 3.84 |
| 16   | 0.957 $\pm$ .112          | 5.02 $\pm$ 0.53  | 19.52 $\pm$ 1.79 |
| 12.2 | 0.139 $\pm$ .052          | 1.84 $\pm$ 0.34  | 7.72 $\pm$ 1.69  |
| 8.2  | -0.015 $\pm$ .025         | 1.05 $\pm$ 0.72  |                  |
| 4    | 0.025 $\pm$ .017          | 0.84 $\pm$ 0.37  |                  |

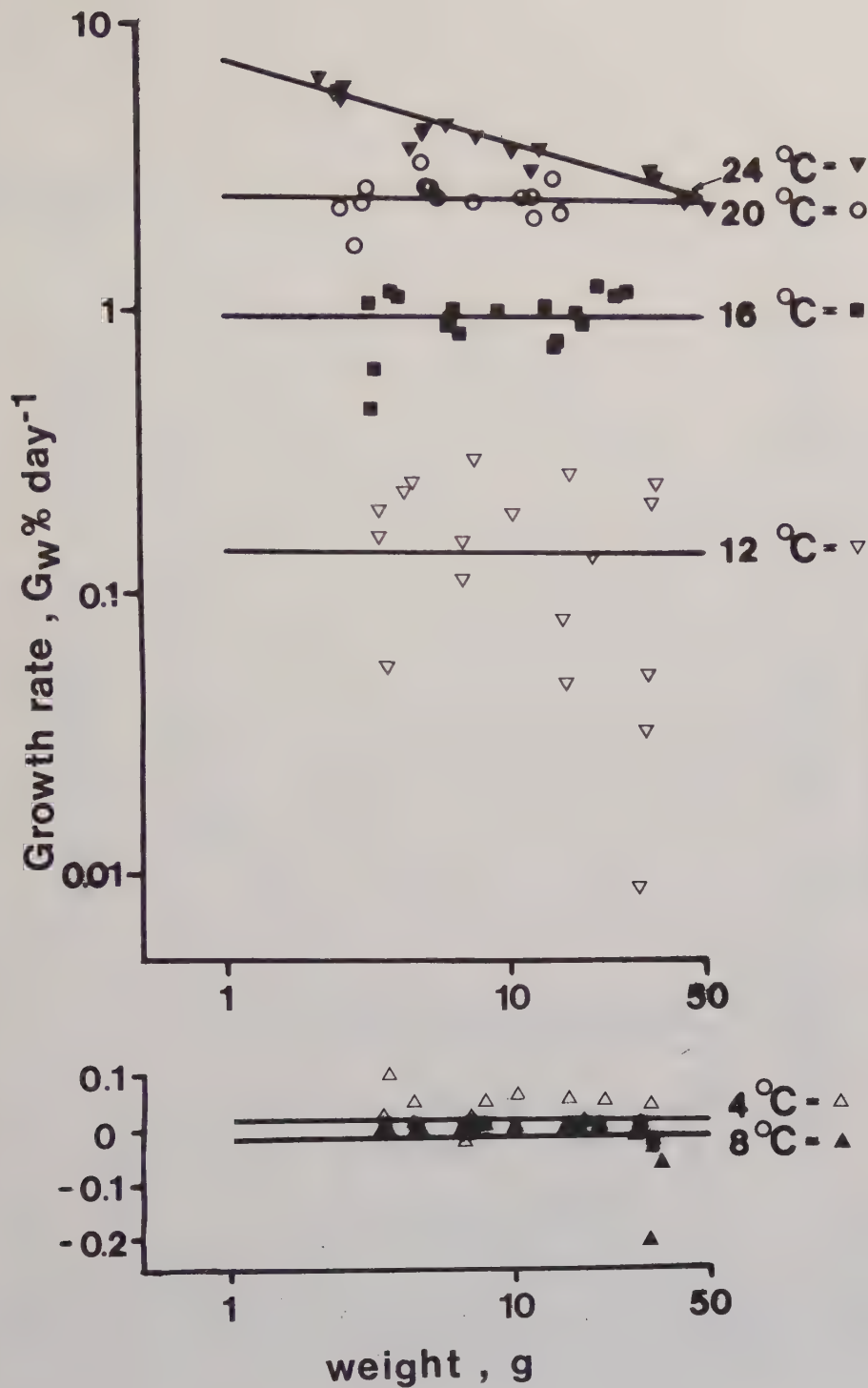


Fig. 1. Relationship between growth rate and mean weight of roach at different temperatures. At 4-20  $^\circ\text{C}$  the lines describe mean values for fish of different weights. At 24  $^\circ\text{C}$  the line is the regression line for the best fit.



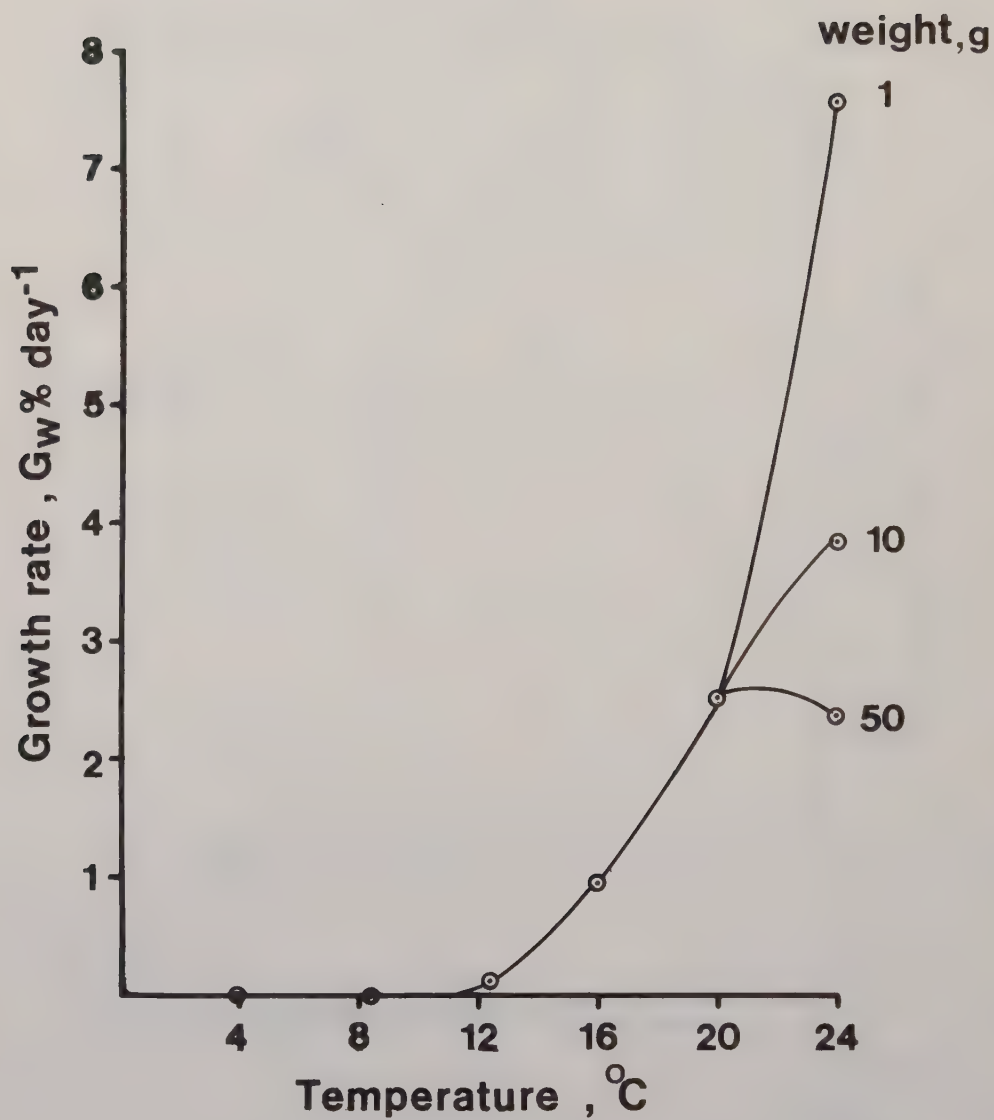


Fig. 2. Relationship between calculated growth rate and temperature for different wights of roach.

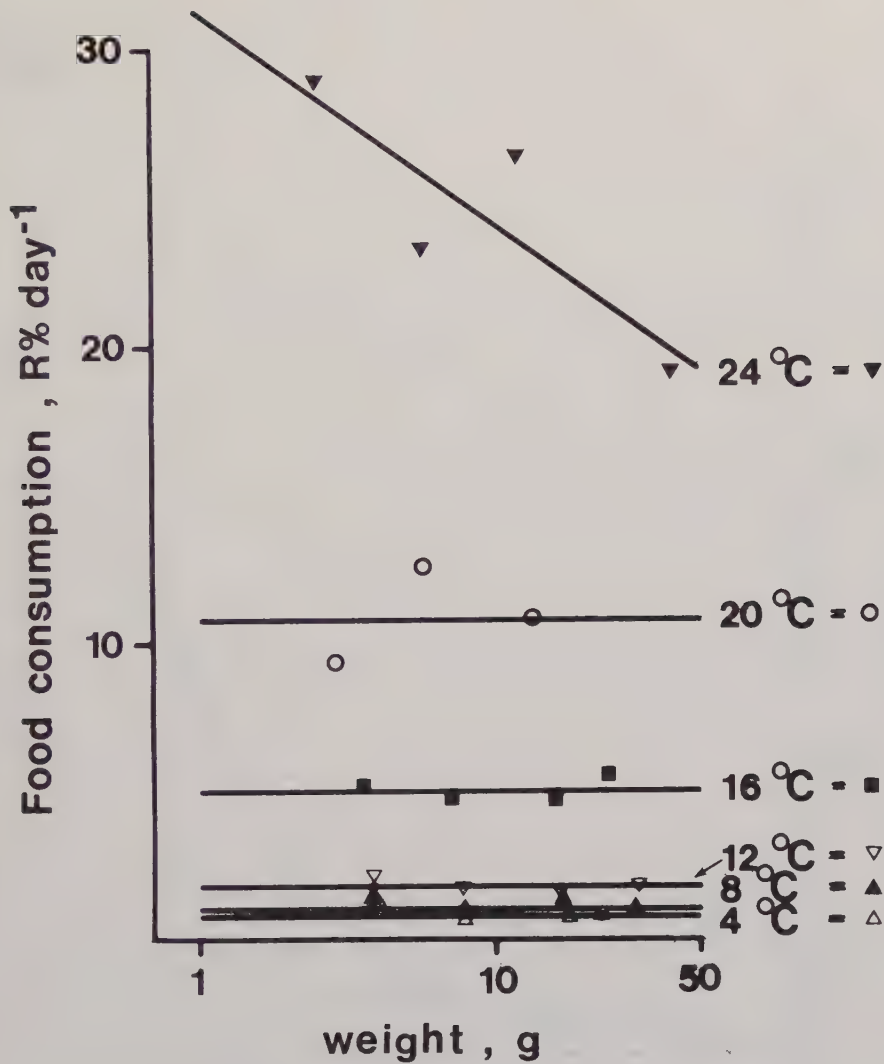


Fig. 3. Relationship between maximum food consumption and mean weight of roach at different temperatures. At 4-20 °C the lines describe mean values for fish of different weights. At 24 °C the line is the regression line for the best fit.

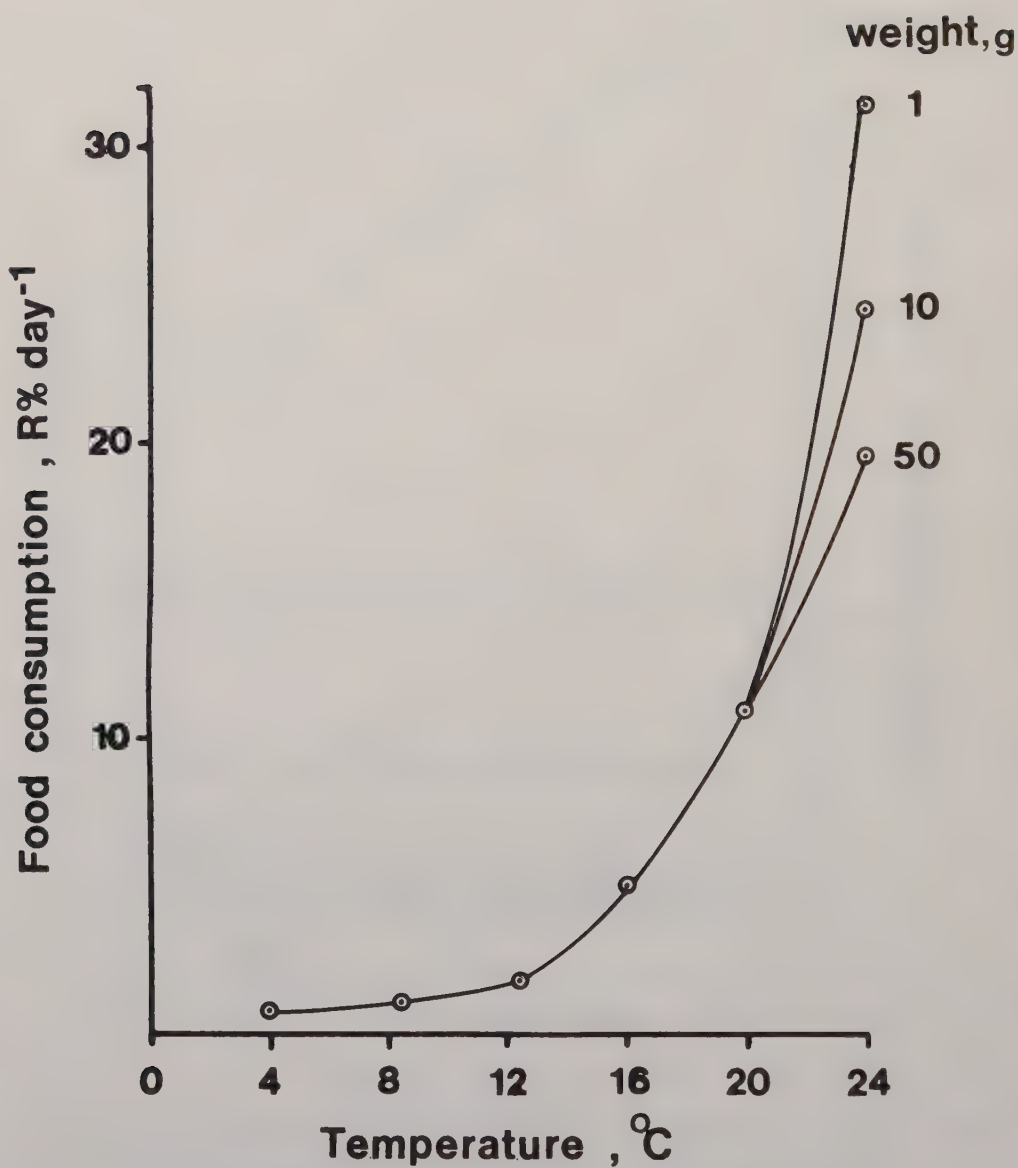


Fig. 4. Relationship between calculated maximum food consumption and temperature for different weights of roach.

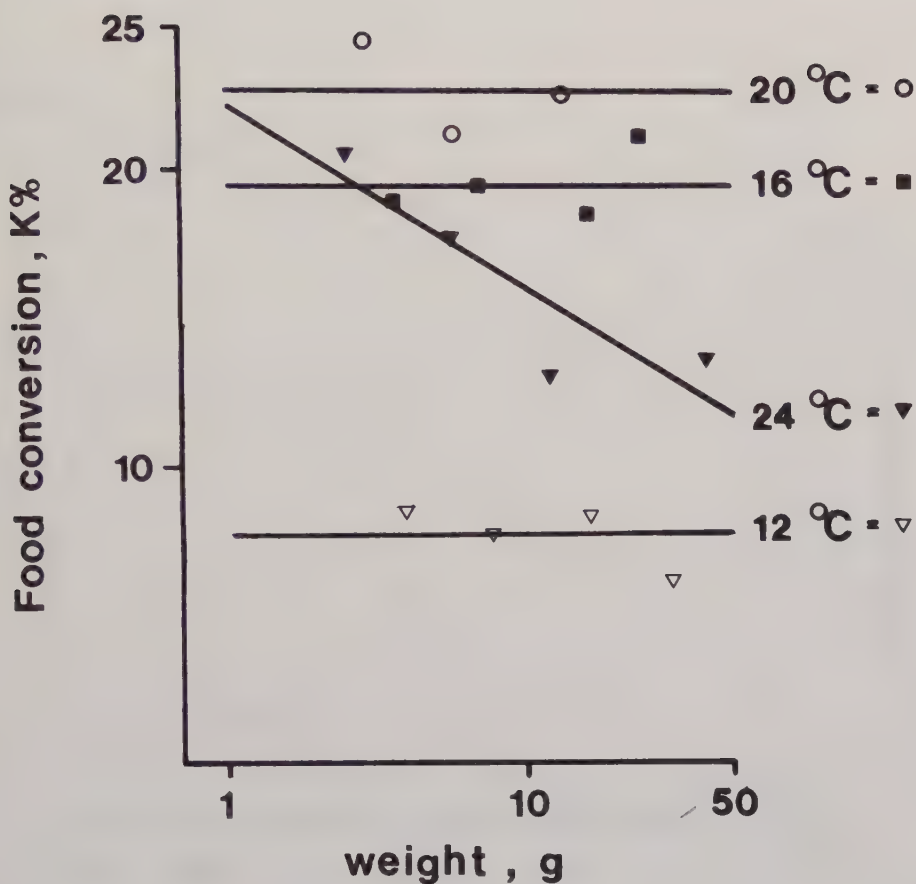


Fig. 5. Relationship between food conversion efficiency and mean weight of roach at different temperatures. At 12-20 °C the lines describe mean values for fish of different weights. At 24 °C the line is the regression line for the best fit.



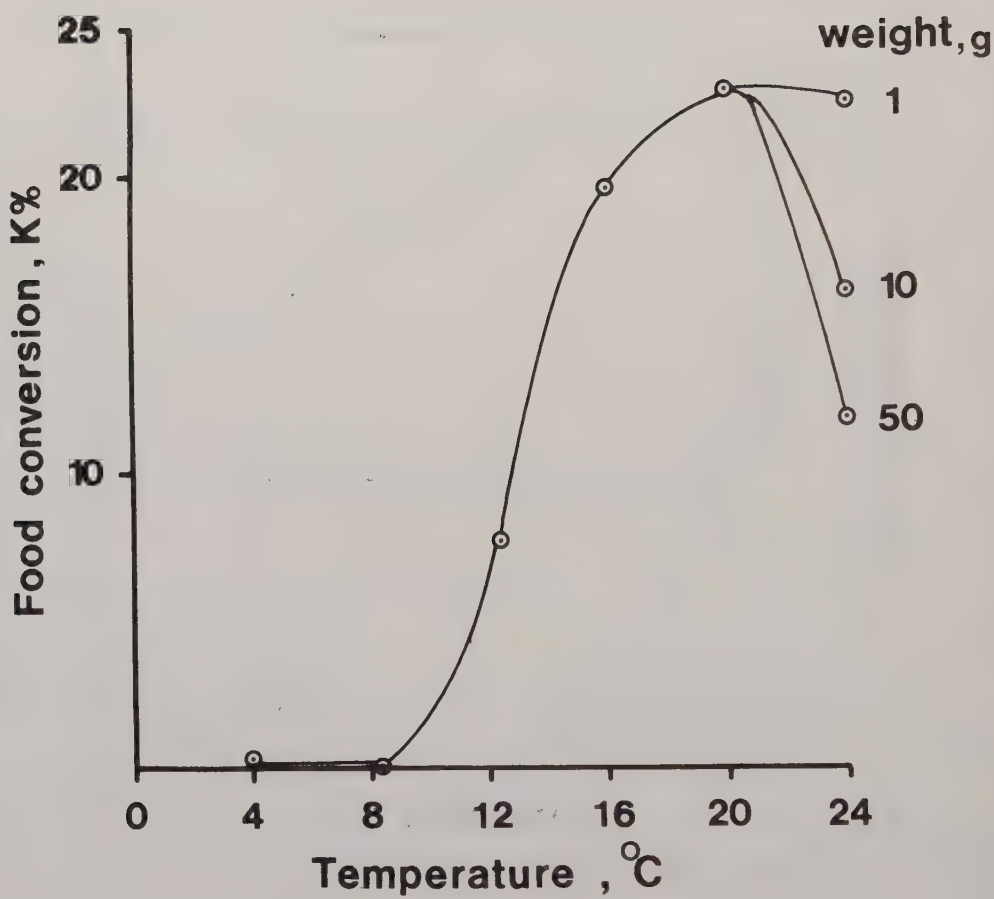


Fig. 6. Relationship between calculated food conversion efficiency and temperature for different weights of roach.

EFFECTS OF RATION SIZE AND TEMPERATURE ON GROWTH AND  
FOOD CONVERSION OF ROACH (*Rutilus rutilus*)

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## SUMMARY

The effect of ration size on the growth and food conversion of roach (Rutilus rutilus) weighing about 2 g, was studied at the temperatures 4, 8, 12, 16, 20 and 24 °C. Growth was fastest at 24 °C. Temperature and ration size influenced growth and food conversion in a complex way. Maximum food conversion (about 30 %) was reached at about 20 °C.

## INTRODUCTION

In a previous work on the energetics of roach, it was shown how temperature and fish-weight influence growth rate, food consumption and food conversion when fish were fed maximum rations of animal food (Lessmark 1983c).

The aim of this study was to estimate the influence of ration size on the growth and food conversion of roach at different temperatures. A similar study was done earlier on perch, Perca fluviatilis (Lessmark 1983b). Some information on the effect of ration size on the growth of roach was given earlier by Winberg (1956).

## METHODS

Fish, weighing about 2 g (range 0.8-4.0 g) were kept in 60 litre aquaria with a continuous through-flow of fresh water. A group of generally five fish were kept in each aquarium at temperatures of 4, 8, 12, 16, 20 and 24 °C. Temperature were co-ordinated with seasonal changes in temperature in the natural environment. The groups of fish were fed varying amounts of food. Details are presented in table 1.

After acclimatization to experimental conditions, each group of roach was fed a defined daily ration of live animal food for a varying number of days. A diet of Daphnia magna was used for all temperatures except for 4 °C, when Chaoborus was used instead. At 24, 20 and 16 °C, the daily ration consisted of four equal sized meals spread over a 12 h period. At 12 and 8 °C, two meals were given daily and at 4 °C, one meal. Prior to the start and termination of an experiment the fish were starved to evacuate the gut.

Replicate experiments were run in two years at temperatures ranging from 12 to 24 °C. To study how season effect growth and food conversion, the experiments were run at different times of the year (Tab. 1).

The experimental set up and realization, handling and weighing of fish and food animals and calculations were the same as those previously described by Lessmark (1983a). Data from a previous study on growth and food conversion for roach on maximum rations has been used in this paper (Lessmark 1983c).

Growth rates were calculated as specific growth rates and expressed as percentage weight-increase per day ( $G_w \text{ \% day}^{-1}$ ). Food consumption was related to body weight and expressed as a percentage of fish weight per day ( $R \text{ \% day}^{-1}$ ). Food conversion efficiency was calculated on a percentage basis and expressed as weight-increase per amount of consumed food ( $K \text{ \%}$ ).  $R$  and  $K$  were estimated on organic dry weight values.

## RESULTS

### Effect of ration-size and temperature

Growth rate increased with ration-size at all temperatures and the curves describing these relationships were fitted by eye (Fig. 1). Highest growth rates were obtained at 24 °C (Fig. 2). Optimum temperature for growth varied with ration and was; 20 °C for daily rations in the range 3.5-11 %. Growth was influenced by temperature and ration-size in a complex way (Fig. 3).

Maintenance ration increased with temperature from less than 1 % at 4 °C, to about 4 % at 24 °C.

Food conversion efficiency was determined by both ration-size and temperature, and the curves describing these relationships were fitted by eye (Fig. 4). At 8 °C, no curve was fitted as there was only one value for food conversion above the maintenance ration. Maximum food conversion (about 30 %) was reached at about 20 °C (Fig. 5,6).

### Effect of food-type

Growth rate was similar on equal rations of the two food-items tested (D. magna and Chaoborus) (Fig. 1).

### Effect of season

Experiments were done in May and November-December at 12 °C, in June and September-October at 16 °C and at other times of the year at 20 and 24 °C (Tab. 1), but results demonstrated that, on equal

rations, season did not influence growth rates (Fig. 1).

## DISCUSSION

Similar growth rates were obtained for the same sized rations of Daphnia and Chaoborus and growth rates did not seem to be dependent on food quality of animal food. However, growth rates were much higher on an animal diet than on a vegetable diet (Lessmark 1983f).

Despite the fact that in some experiments, the roach had an excess of food, consumption and growth rates were higher when the food was limited and given in small but frequent rations. In the experiments where there was an excess of food (Lessmark 1983c), the fish were fed Chaoborus, whereas Daphnia was used as food in the other experiments. If the roach had more difficulty catching and handling Chaoborus, this would explain the lower consumption and growth rates in these experiments. However, at 4 °C, Chaoborus was used in all experiments and consumption rates were lower with a continuous, excess food-supply than with occasional, smaller rations. It is possible that the periodical lack of food stimulated consumption more because an abrupt change in food supply is visually more stimulating than unchanged access to food. Thus maximum food consumption and growth rates for roach might have been different, from in experiments with excess of Chaoborus, if the kind of food and feeding frequency had been different. The isopleth curves would then also have been slightly different.

Growth rate values on specific rations in this study, correlated positively with three of the five values Winberg (1956) quoted for the growth of roach at 20 and 24 °C. Two of Winberg's values deviated considerably.

The results of this study do not agree entirely with the general opinion that the optimum temperature for growth decreases when ration-size decreases (See references in Lessmark 1983b). At ration sizes lower than 7 %, 16 °C was better for growth than 24 °C (Fig. 2). For larger rations, 24 °C was more favourable than 16 °C. In a broad range of rations above maintenance, 20 °C was the best temperature for both growth and food conversion. When roach were fed maximum rations in another study (Lessmark 1983c), highest food conversion were attained at 20 °C. Perch also attained highest growth and food conversion for a range of ration-sizes at a specific temperature (Lessmark 1983b). I gave a possible explanation for this,



which might also explain why food conversion for roach was most efficient at a specific temperature.

To explain vertical migration of zooplankton, McLaren (1963) suggested that because of reduced metabolic costs at lower temperatures, it would be favourable to migrate from a warm feeding habitat to cooler water for digesting the food and in that way get a higher net gain for the consumed food. Brett (1971) used McLaren's hypothesis to explain the vertical migration of sockeye salmon (Onchorynchus nerka) in a temperature stratified lake. Biette and Geen (1980) tested McLaren's hypothesis on sockeye salmon in laboratory experiments and concluded that fish ingesting moderate rations and undergoing diel migrations from cooler deep water to warmer surface waters, are likely to grow more rapidly than fish in a constant temperature.

The positive effect on growth of vertical migration and lower metabolic costs in a cooler habitat, would be reduced for roach and perch (Lessmark 1983a,b) because food conversion efficiency would be reduced, as growth was most rapid over a wide ration range, and food conversion was most efficient at 20 °C.

Giguère and Dill (1980) made a similar conclusion as regards the migration of Chaoborus trivittatus, because assimilation efficiency of food was temperature-dependent.

If McLaren's hypothesis were valid for roach, roach would sometimes prefer low temperatures but roach are never found in cold water in stratified lakes with a maximum temperature of about 20 °C (Lessmark 1983e).

For walleye (Stizostedion vitreum vitreum), food conversion was lower in cyclic temperatures than at a constant temperature (Kelso 1972) and for maomao fish (Abudefduf abdominalis), cyclic temperature did not have a growth advantage over constant temperatures under limited rations (Medvick 1979). Short-time deviations from a given temperature lead to major shifts in metabolism, produce acid-base imbalance and cause disturbances in fluid electrolyte regulation (Crawshaw 1977), which reduces the advantage of cyclic temperatures. Roach and perch, like walleye, maomao and Chaoborus trivittatus, do not fit McLaren's hypothesis (op cit) which is not valid for all species.

It can be concluded that roach is physiologically best adapted to utilize food at 20 °C, and the type of animal food and season is of little or no significance to growth and food conversion efficiency in roach.

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- e. The combined effects of temperature, food quantity and food quality on interspecific competition between perch (Perca fluviatilis) and roach (Rutilus rutilus). Manuscript.
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Table 1. Experimental conditions for studying growth rate and food conversion of roach fed varying ration-sizes at various temperatures.

| Temperature<br>°C | Time of year    | Duration of<br>experiments<br>days | Number of<br>experiments |
|-------------------|-----------------|------------------------------------|--------------------------|
| 4                 | Feb.-Mar.       | 20                                 | 4                        |
| 8                 | Apr.-May        | 17                                 | 3                        |
| 12                | May,Nov.-Dec.   | 15-27                              | 8                        |
| 16                | June,Sept.-Oct. | 10-14                              | 10                       |
| 20                | July,Sept.      | 9-10                               | 7                        |
| 24                | July,Aug.-Sept. | 9                                  | 7                        |

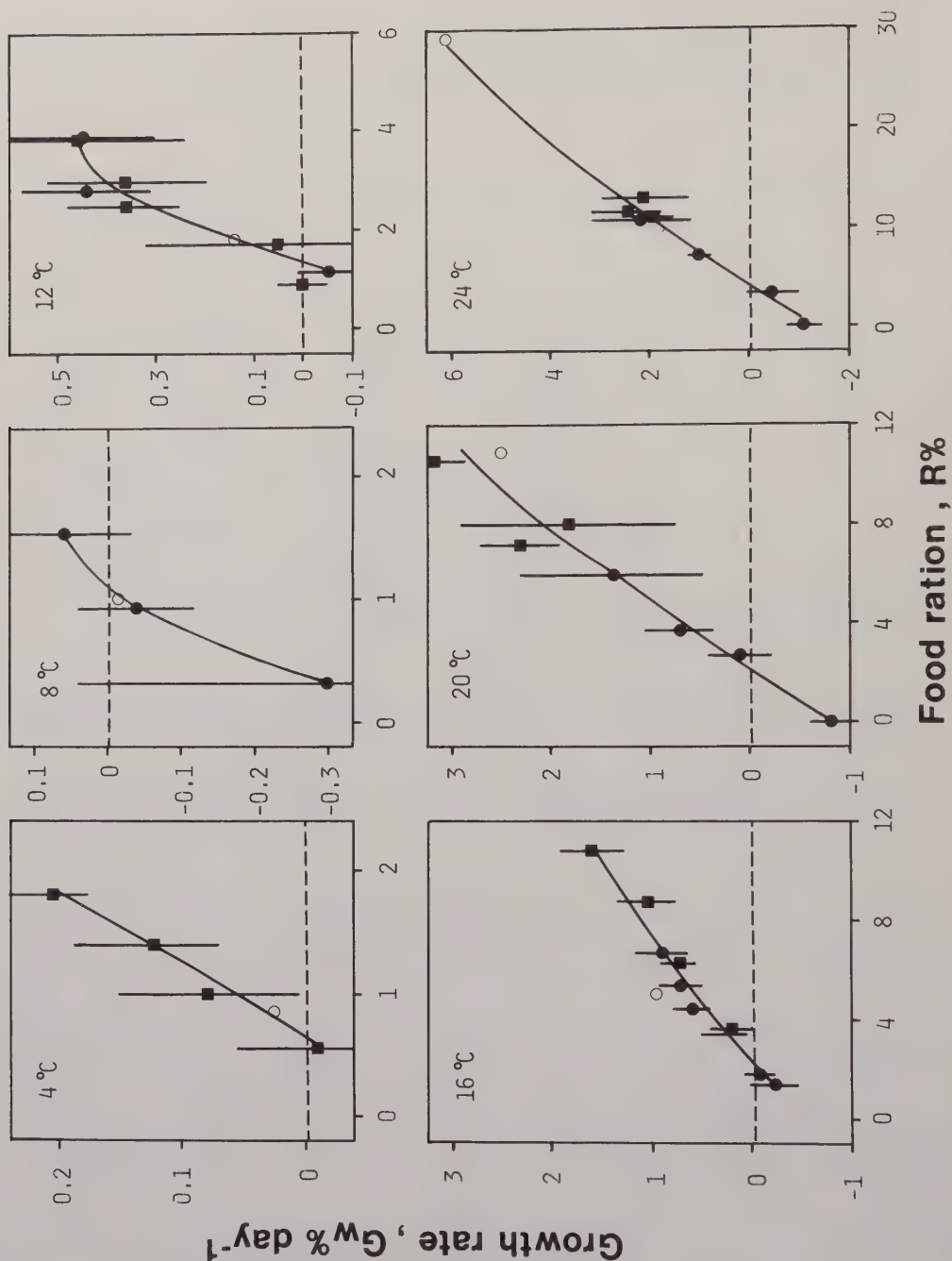


Fig. 1. Relationship between growth rate ( $\pm$  95 % C.L.) and ration size at different temperatures for roach weighing about 2 g. Solid circles and squares represent results from different years. Empty circles represent results on maximum rations of the dipteran larvae Chaoborus (Lessmark 1983c)

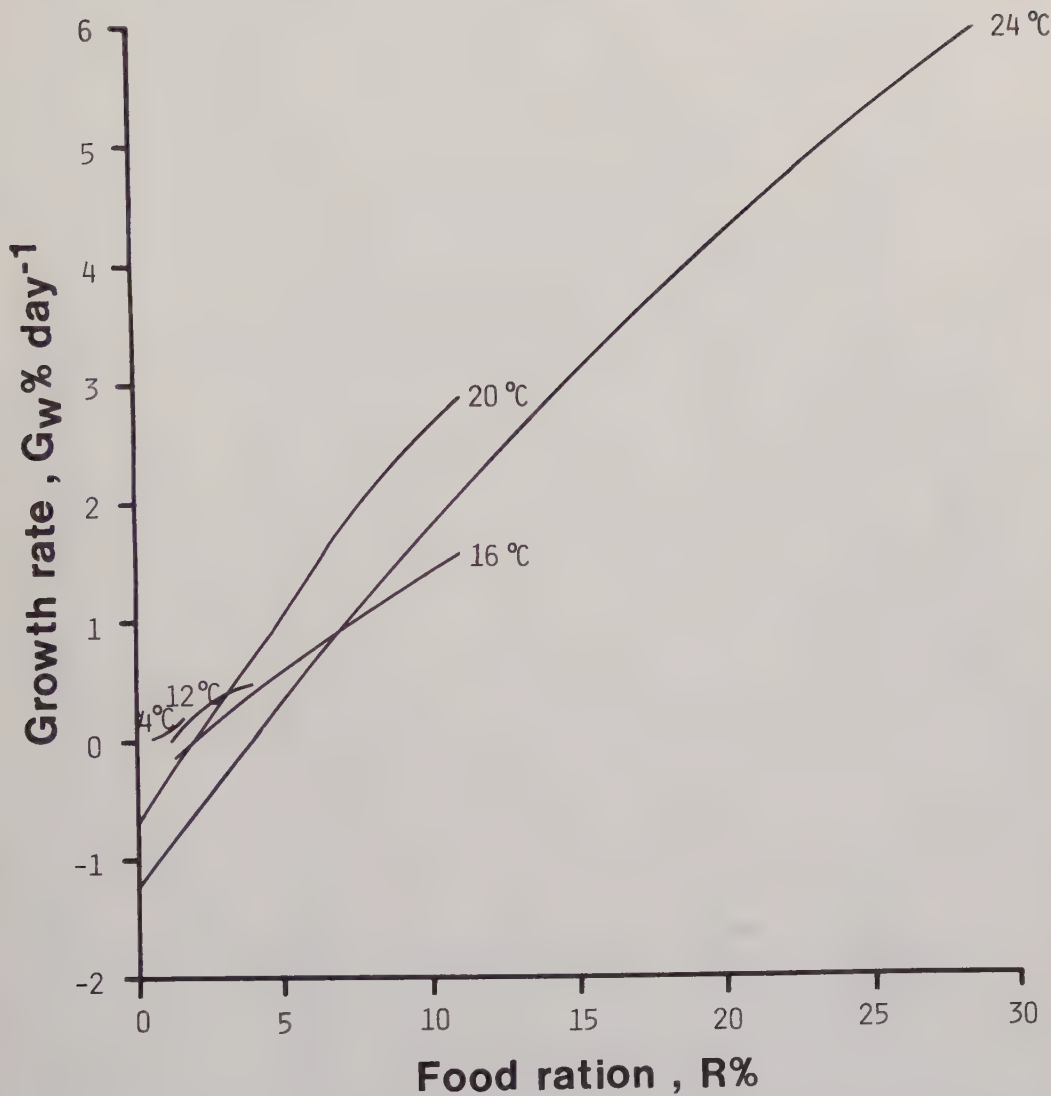


Fig. 2. Growth rate of roach at different temperatures and ration sizes. Curves are the same as in figure 1, but here drawn to the same scale on the axes.



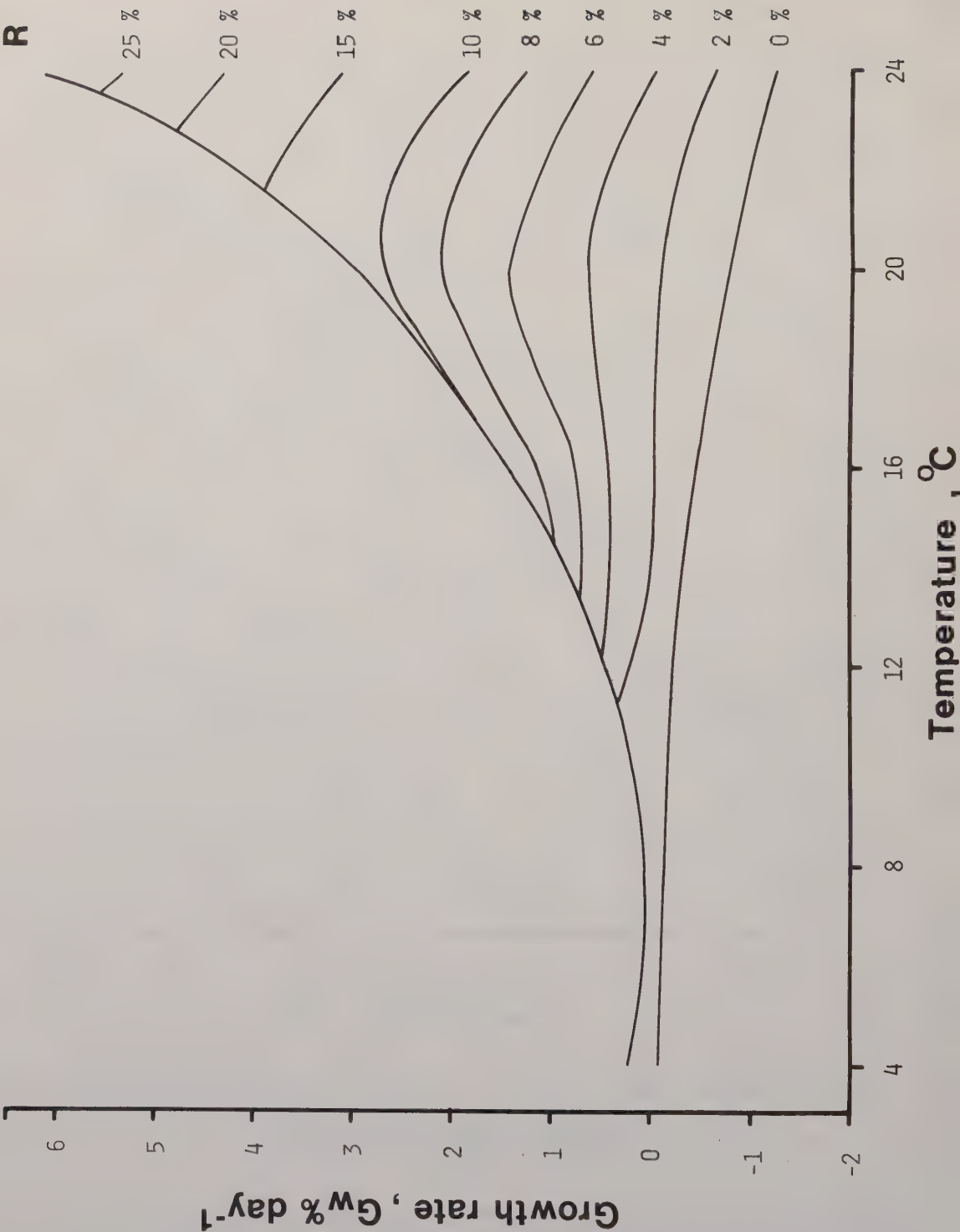
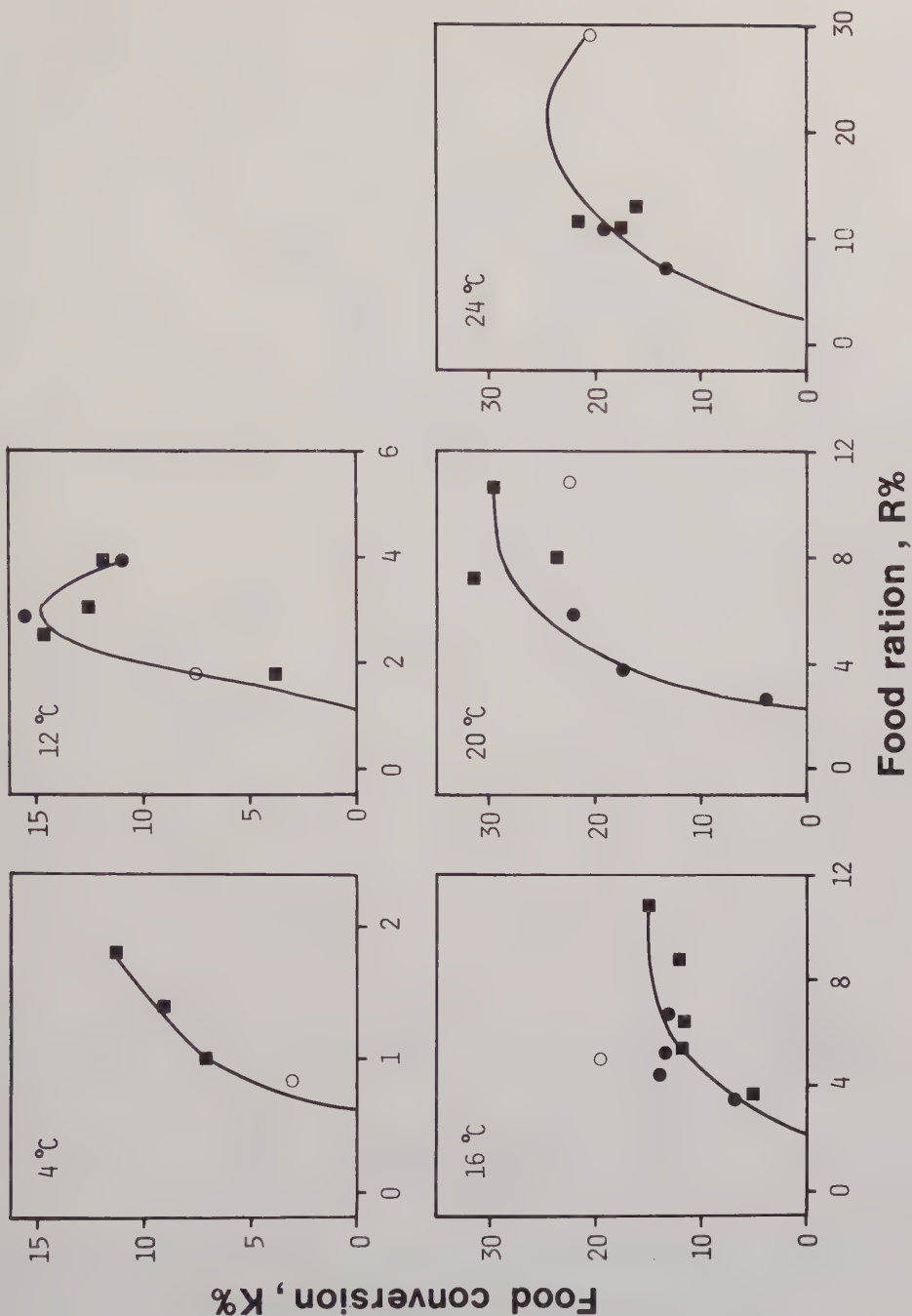


Fig. 3. Growth rate of roach at different temperatures and ration sizes (R). Curves were fitted from data in figure 1.



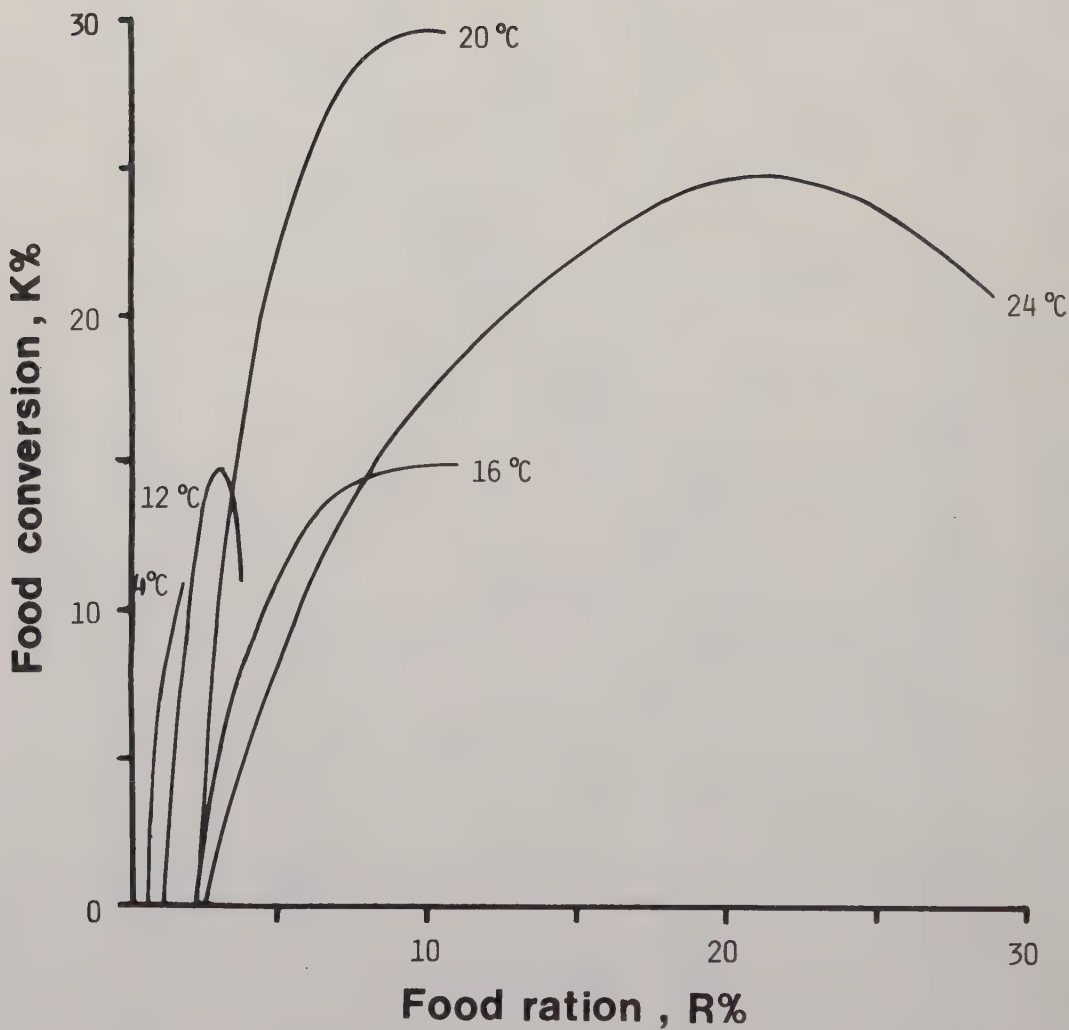


Fig. 5. Food conversion efficiency of roach at different temperatures and ration sizes. Curves are the same as in figure 4 but here drawn with the same scale on the axes.

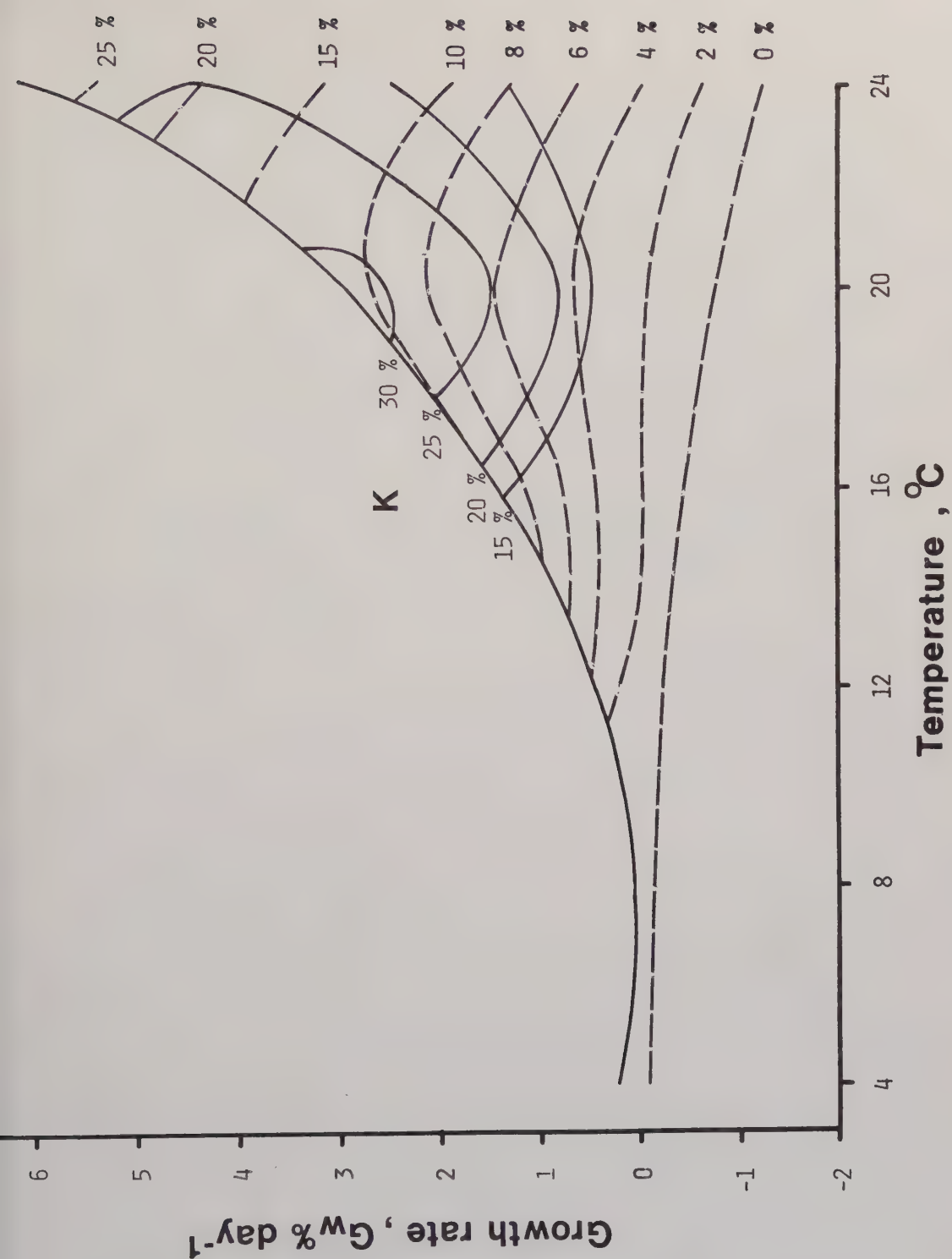


Fig. 6. Isopleths for food conversion efficiency (K) of roach at different ration sizes (R) and temperatures.





THE COMBINED EFFECTS OF TEMPERATURE, FOOD QUANTITY  
AND FOOD QUALITY ON INTERSPECIFIC COMPETITION  
BETWEEN PERCH (*Perca fluviatilis*) AND ROACH  
(*Rutilus rutilus*)

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## SUMMARY

This paper describes perch and roach adaptation to temperature, food-quality and food-quantity and evaluates influence on feeding strategies and how they are favoured at different temperatures and structure of food resources. Food consumption, growth and food conversion on varying ration sizes and at various temperatures were estimated in laboratory experiments.

On maximum rations of Chaoborus larvae, in a 4-24 °C temperature-range, perch consumed more food than equal sized roach at temperatures between 4 and 22 °C and grew faster than roach over the entire temperature-range. The relative difference between the growth rates for perch and roach decreased as the temperature increased. Perch is thus adapted to lower temperatures than roach and temperature regime in Swedish lakes favours perch more than roach.

Perch has a strictly carnivorous diet, whereas roach is able to utilize vegetable food when animal food is in short supply. Roach prefer animal food however, and grow faster on animal food diet. Omnivory is disadvantageous for roach in that they are not able to utilize animal food as efficiently as the purely carnivorous perch. In a wide size-range of Daphnia and Chaoborus rations, perch was a more efficient food converter than roach. Physiological adaptation influences foraging behaviour and feeding strategies under natural conditions. Perch is a fast-moving hunter and consumes bigger prey than roach, which can be better characterised as a slow-moving cropper that consumes smaller prey and plant material. The smallest profitable prey for perch is thus larger than the smallest for roach.

These varying strategies influence interspecific competition, favouring one or the other depending on abundance and quality of food. Perch is relatively more favoured in lakes with sparse fish populations and high abundance of animal food, and the reverse conditions are relatively more favourable to roach which can then utilize vegetable food. Thus perch are more favoured in the initial stages of succession when a new environment is colonised by fish, as for example after heavy fish kills and in the creation of new waters.

## INTRODUCTION

Temperature is one of the most important abiotic factors determining the success of poikilotherm organisms in the physical environment, because it regulates the speed of vital processes like food consumption, food conversion and growth. Generally, metabolism increases with an increase in temperature but different species are adapted to different temperatures and their physiological optimum temperatures concerning e.g. growth rate differ. A high temperature can be lethal for one species but optimal for another. In the same way a low temperature can be optimal for one species, but life processes of an other species may be strongly reduced. Effects of big differences in temperature adaptation is thus obvious. Small differences in temperature adaptation, however, have less dramatic results but are nevertheless of great significance for the relative success or dominance of certain various species in an environment.

Due to a lack of more detailed information on temperature adaptation, generalized words such as cold-water or warm-water have been used to categorize fish species. Eurythermic describes species that have broad temperature tolerance limits and stenothermic have been used to describe species with narrow temperature tolerance limits. However, the artificiality of a relative system such as this, becomes evident when an attempt is made to classify fish from various geographic regions. Species adapted to the extremities of the temperature range are easily categorized as cold- or warm-water species, but for less extreme temperatures these categories are inadequate.

In temperate lakes, where annual temperatures fluctuates widely and where vertical temperature stratification is common, temperature influences niche and resource partitioning among the different species with regard to food, habitat and season.

Demand for food, food consumption and growth are regulated by temperature. Food consumption is however often limited by food competition. It follows that temperature, favours certain species depending on the degree of temperature adaptation of the competing species. If one species were adapted to a low temperature and another to high and they share limited food resources, competition between them would be low-level at their respective temperature optima and most intensive somewhere between the two temperature optima. By controlling food competition, degree of temperature adaptation would also influence species-abundance.

The adaptation of different species to varying food-quantities and the fact that maximum growth rates vary, are other important

factors affecting food-choice, feeding-niche and niche partitioning. Depending on the quantity and quality of food in a lake, certain fish species would be favoured. Thus, temperature and food-ration adaptation interact to influence the success of fish species in a lake and the degree of interactions between species.

However, adaptation to temperature and ration-size are not the only factors determining the success of a certain species. The most important process is not to eat but to grow. Food conversion efficiency must be considered, and also the possibility that different species might be adapted to different combinations of temperature and ration-size, and thereby be favoured at different intervals of temperature and ration-sizes.

All these physiological adaptations to temperature, amount of food and food conversion must be of importance for which species that will become most abundant in a lake, and also for the way interactions like food competition and predation will take place. Physiological adaptation will also influence the foraging behaviour of the fish.

This study takes up the combined effects of temperature, food-quantity and food-quality on the interspecific competition between perch (Perca fluviatilis) and roach (Rutilus rutilus). These are two of the most common fish species in Scandinavia. They co-habit thousands of lakes and often dominate the fish fauna by their numbers, especially in the shallow, polymictic lakes of southern Sweden. Roach is generally most abundant and there is evidence that there is strong competition between the two species (Lessmark 1983h).

The aim of this study is to investigate how perch and roach are adapted to different temperatures and to food-quantity and quality. An attempt is made to investigate which species is relatively most favoured at different combinations of temperature and food-ration, and to evaluate how this affects foraging, food competition and abundance relationships between the two species in different lakes.

## METHODS

Data on food consumption, growth and food conversion at different temperatures, rations and weights of perch and roach have previously been presented (Lessmark 1983a,b,c,d). Details of experimental design and methods are given in these papers and here only a summarized description is presented.

The fish were kept at constant temperatures and were fed live animal food, Chaoborus or Daphnia. Growth rates were calculated as specific growth rate and expressed as percentage weight increase per day ( $G_w \% \text{ day}^{-1}$ ). Food consumption was related to body-weight and expressed as a percentage of fish-weight per day ( $R \% \text{ day}^{-1}$ ). Food conversion efficiency was calculated on a percentage basis and expressed as weight-increase per amount of consumed food ( $K \%$ ).  $R$  and  $K$  were estimated from organic dry weight values. The experiments at a particular temperature were run simultaneously for perch and roach and the fish were treated identically.

To calculate the theoretical maximum weight-increase on maximum food supply for fish with an initial weight of 1 g, I used the values for maximum growth rates at specific temperatures and weights of fish estimated in laboratory experiments.

- |     |                           |                      |
|-----|---------------------------|----------------------|
| (1) | at a temperature of 20 °C | for a 100 day period |
| (2) | "                         | 16 "                 |
| (3) | "                         | 12.2 "               |

Calculations were done step-wise at 10-days intervals and growth rates were adjusted to the changing fish-weights during these intervals.

From data on food consumption in laboratory experiments, I calculated the number of different-sized prey that fish of different sizes needed to consume to attain maximum daily consumption at 20 °C. I also calculated the time-limit per prey-item if maximum daily food consumption were to be reached, assuming that there was sufficient light for 18 hours foraging per day. To investigate the effect of temperature, I estimated the number different-sized prey that a 10 g perch and roach would have to consume to attain maximum food consumption at different temperatures.

I recorded the vertical distribution and temperature preference of perch and roach during summer in three thermally stratified lakes by using gill-nets set at various depths (Lessmark 1983h). Temperature and oxygen recordings were done at the same time.

## RESULTS

### Food consumption

Maximum food consumption for 10 g fish with food supply in excess was higher for perch than for roach at temperatures below about 22 °C (Fig. 1); but higher for roach at temperatures over 22 °C. It



can be concluded from this that roach is physiologically adapted to higher temperatures than perch is. However, it is not possible to estimate the optimum temperature for consumption, which is above 24 °C for both perch and roach weighing 10 g. Perch and roach seldom attain maximum temperature for consumption in Scandinavian lakes, where the temperature rarely exceeds 24 °C. The studied temperature interval can be regarded as relevant for evaluating the feeding ecology of perch and roach in Swedish lakes.

The number of prey and the time-limit per prey needed for a fish to attain maximum daily food consumption at 20 °C, depends on the fish species and on the weight of the fish and the size of the prey (Fig. 2).

Temperature also determines the number of prey necessary if maximum food consumption is to be attained (Fig. 3).

### Growth

Maximum growth rate was higher for perch than for roach at all temperatures (Fig. 4). The relative differences in growth rate between similar-sized perch and roach decreased with increasing temperatures. For a 10 g perch, the growth rate is about 3 times that for the same sized roach at 12 °C, double that of roach at 20 °C and at 24 °C it is 1.5 times higher than that for a 10 g roach. At about 24 °C the increase of growth rate declined for perch but not for roach. Optimum temperature for growth is thus higher for roach than perch, but in the size-range in this study, it seldom occurs that either of the two species attains maximum growth rates under natural conditions in Swedish lakes. It is important to stress that roach is relatively more favoured compared to perch when temperature increases. Below 12 °C, when growth of roach ceases almost completely perch continues to grow slowly. The growth rate for a 10 g roach at 16 °C is the same as that for a 10 g perch at 13 °C.

Perch grew faster than roach on equal rations, except when rations were close to maintenance at 20 and 24 °C (Fig. 5). The difference between the growth rates for the two species became smaller on low rations. When no food was consumed at 20 and 24 °C, perch lost more weight than roach.

In theory, perch with an initial weight of 1 g would, at 20 °C with maximum growth rate after 100 days weigh 11 times more than roach under the same conditions, and at 16 °C the perch would weigh 7.5 times more than the roach (Fig. 6). At 12 °C the weight-increase

will be small for both species, for perch from 1 to 3.6 g and for roach from 1 to 1.5 g.

#### Food conversion

At all temperatures, food conversion on maximum rations was more efficient for perch than for roach (Fig. 7). For 10 g fish, the optimum temperature was about 18 °C for perch and 20 °C for roach. Thus, on maximum rations perch grow faster than roach and utilize the food better for growth. Even on a broad range of ration sizes, perch was a more efficient food converter than roach (Fig. 8).

#### Temperature preference in stratified lakes

For both species, optimum temperatures are seldom reached in Swedish lakes and results from the temperature preference investigation in stratified lakes, agreed with the laboratory experiment results. Both perch and roach were most abundant in the upper, warmer epilimnion water (Fig. 9). Oxygen conditions in deeper water were not limiting for the fish distribution.

### DISCUSSION

#### Temperature adaptation

Roach is adapted to higher temperatures as regards optimum food consumption, food conversion and growth than perch is. This physiological adaptations influence habitat selection, seasonal activity, geographical distribution and spawning period.

The temperature in the southern Swedish lakes where I studied the habitat selection of perch and roach, is below optimum temperature for these species, and too low to result in temperature-induced habitat partitioning. However, in warmer, temperature stratified lakes in southern Europe, temperature might induce habitat partitioning between perch and roach.

The geographical distribution of perch and roach reflects the differences in temperature adaptation between these species. In Sweden, the distribution of perch is more northerly, at higher altitudes than roach is found (Ekman 1922). On the northern outskirts of the distribution area, roach occurs in small, isolated lakes which are warmed up more in the summer than the larger and deeper lakes located downstream where roach is absent (Svårdson 1976). On the

outskirts of their distribution areas, perch and roach are found during the summer in the warmest water, in shallow bays very close to the shore (Lindström and Bergstrand 1979, Filipsson 1980).

Differences in adaptation to temperature also reflected the temperature and time of spawning for the two species. In Lake Sövdborgssjön, southern Sweden, perch spawned in April in 1982, at a temperature of 10 °C and roach in May, at a temperature of 17-18 °C.

The temperature in Swedish lakes, which seldom exceeds 20 °C, favours perch more than roach. The growth season is longer for perch than roach. If temperature were the only factor determining the success of these species in Swedish lakes, perch would always be favoured over roach.

### Food conversion

Food conversion is more efficient in perch than in roach. This might depend on the following: (1) either that perch assimilates food more efficiently than roach, or (2) metabolic costs are higher for roach than for perch as regards processes such as "apparent specific dynamic action" (term used by Beamish 1974, quoted by Elliott 1979) (including e.g. costs for digestion, assimilation, deposition and deamination), or (3) a combination of these factors. That perch is a better food converter than roach cannot depend on higher metabolic demand for roach than perch, since the differences in growth rate between the two species was not constant when the ration-size varied. To the contrary, it is more likely that metabolic demand is higher for perch than for roach, as, on low rations and when starved at 20 and 24 °C, perch lost more weight than roach. On low rations, perch swam more actively than roach, probably expending more energy on locomotion. Thus, differences in metabolic costs for roach and perch, are probably influenced by the different behaviour of the two species.

Differences between perch and roach as regards food conversion, however, most likely result from different digestive systems. Roach lacks acid secretion and the enzyme pepsin, which decomposes protein at low pH (Kapoor et al. 1975). It is therefore likely that the digestion of proteins is less efficient in roach and that proteins are only partly assimilated. Roach commonly consumes plant material, when animal food is in short supply (Lessmark 1983f,h) and has a digestive system and metabolic system adapted to a plant diet rich in carbohydrates. Perch, on the other hand consumes only

animal food, which has a relatively high protein content compared to vegetable food, and the secretion of acid and pepsin is part of the digestive system of this species. That roach is a "food generalist" might be negative in that animal food is not used as efficiently by roach as by more carnivorous species such as perch. If this were not so, it would always be better to be adapted to be omnivorous than to be specialized either to pure carnivory or herbivory.

I maintain, therefore, that the difference in food conversion efficiency between perch and roach is mainly dependent on efficient digestion of animal food.

#### Ration-size adaptation

Perch is physiologically adapted to consume more food and to grow faster than roach. This can explain differences in the feeding strategy of the two species. In several lakes, it was found (Lessmark 1983h) that perch generally consumes larger prey and grows faster than roach. In laboratory experiments, roach consumed smaller zooplankton than similar-sized perch (Lessmark 1983g). The smallest zooplankton consumed by a 7 cm long roach was 0.3 mm and the corresponding size for perch was 0.5 mm. This difference between the two species with regard to the smallest item consumed became larger for larger fish. 17 cm long roach consumed the same-sized prey as 7 cm long roach. For perch, however, the size of the smallest zooplankton consumed increased when the size of the fish increased. This discrepancy was true under natural conditions as well (Lessmark 1983h). Roach commonly consumes zooplankton and other small prey throughout its life, whereas perch switches to larger prey items as its weight increases. Since perch can only handle a certain number of prey in a limited amount of time, it cannot increase the number of prey-items to maintain maximum consumption when its body weight increases, but must instead consume larger items of prey if maximum consumption is to be attained. At lower temperatures it seems easier for perch to attain maximum consumption on smaller prey items than at higher temperatures.

Like perch, larger roach cannot maintain maximum consumption by increasing the number of small prey items. They can, however, compensate by consuming plant material. Plant material is more common in the diet of large roach than in the diet of small roach (Lessmark 1983h). Roach prefers animal food to plant food, and also attains higher growth rates on a purely animal diet. In laboratory experiments, maximum growth rate on a diet of blue-green algae was 0.9 %



day<sup>-1</sup> (Lessmark 1983f). However, when animal food is in short supply, roach shift to a more vegetable diet. Sometimes roach have a purely vegetable diet, but generally a vegetable dominated diet consists of a minor part of animal food. Roach may primarily consume plants but may require animal proteins in relatively small quantities. This may be one reason why it is more profitable for roach to consume smaller prey than for perch.

It might be easier for roach to attain maximum consumption on small items of animal food at lower temperatures than at higher temperatures. When the temperature decreased in Lake Sövdeborgssjön zooplankton became a greater proportion of the diet of roach compared to higher temperatures when primarily plant-material was consumed (Persson 1983). This shift in feeding strategy could not have been due to greater abundance of zooplankton, since the amount of zooplankton decreased when the temperature decreased.

Differences in the feeding strategies of perch and roach under natural conditions is, thus, not only a result of adaptation to different amounts of food, but is also correlated with differences in the conversion efficiency of animal food.

Daily maximum food consumption is also determined by the quality of food. Fed with Chara, roach consumed an amount corresponding to about 35 % of the fishes weight per day at 20 °C (Hofer and Niederholzer 1980), whereas intake of meal worms was much less, about 5 %. At several temperatures, when roach were fed with several small rations of Daphnia, food consumption was higher than when they were fed an excess of Chaoborus (Lessmark 1983c,d). The differences in the consumption rates of perch and roach, may not have been the same if another type of animal food had been tested. However, comparison of consumption rates must be done with the same type of food, and I suspect that the general conclusion on differences in adaptation to ration-size between perch and roach would have been the same even for other types of animal food.

## Behaviour

Roach is adapted to consume less food and smaller prey than perch and to consume plant material, which perch never does. These differences are reflected in the foraging behaviour of the two species (Lessmark 1983g). Roach swims slowly and picks mobile and immobile food-items. Perch only preys on mobile items and generally



rushes at the prey. Roach can be characterized as a cropper and perch as a hunter. The foraging behaviour of perch must be more energy-consuming than that of roach, which means that the gross gain per prey must be bigger for perch than for roach if there is to be a net gain for growth.

In aquarium experiments, when there was a shortage of food, perch swam around agitatedly whereas roach moved more slowly and spent less energy on food searching (Lessmark 1983b,d). When the fish were kept without food, perch lost more weight than roach. This difference in behaviour is probably a result of the fact that perch is adapted to consume more food and grow faster than roach, and must attain a certain growth to survive and reproduce. When animal food is scarce, roach shifts to a more vegetable diet, which foraging requires less energy than hunting.

### Conclusion

The foraging behaviour, food-choice and growth rate show that perch is adapted to more energy-rich food than roach. The low respectively high energy feeding adaptation of roach and perch will favour them differently depending on the structure of food resources in a lake. When the fish populations of a lake are sparse, the quantity of food per fish is higher and larger zooplankton are more common than when the fish populations are denser. Perch is therefore relatively more favoured than roach when abundance of fish is low, because perch is able to use more food and grow faster than roach. Roach, however, is relatively more favoured when abundance of fish is high, because roach is adapted to consume less food than perch and use smaller zooplankton than perch and switch to a vegetable diet when animal food is in short supply.

Perch is thus more favoured than roach in the early stages of colonisation of newly-formed waters and after heavy fish-kills. Later, when the fish populations become denser, roach is more favoured and the perch population will decline.

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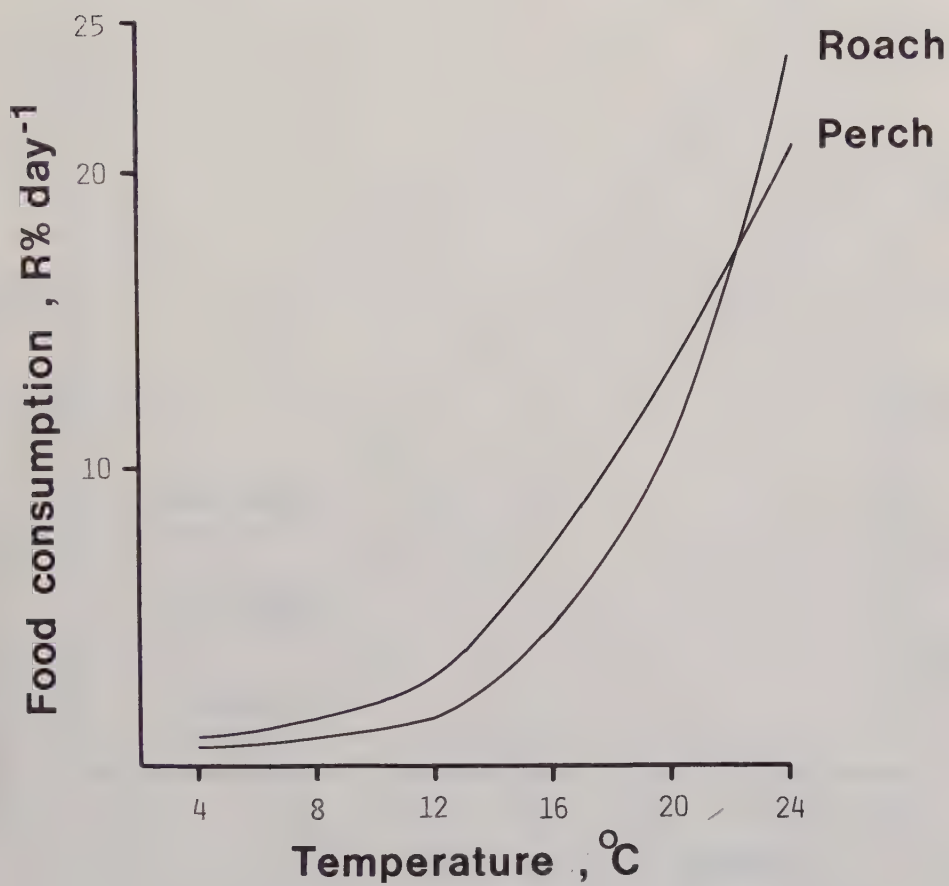


Fig. 1. Relationship between maximum food consumption and temperature for 10 g perch and roach fed maximum rations of the diptera larvae Chaoborus.

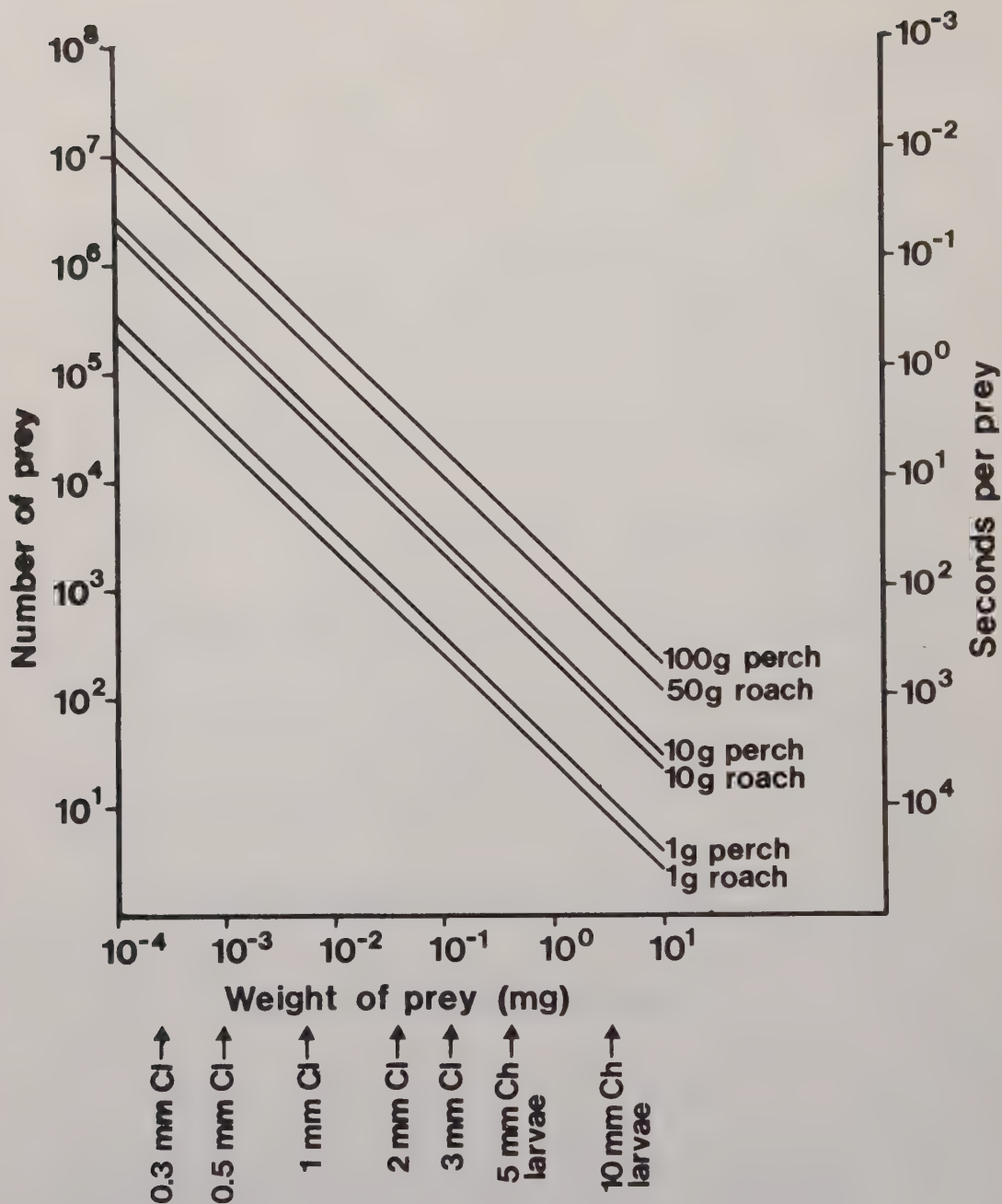


Fig. 2. Number of different-sized preys which perch and roach of different weights have to consume per day to attain maximum daily food consumption, and the calculated time-limit per prey of different sizes if maximum consumption is to be attained. Cl = Cladocerans, Ch = Chironomid larvae. Weight of prey is given in organic dry weight and of fish in fresh weight.

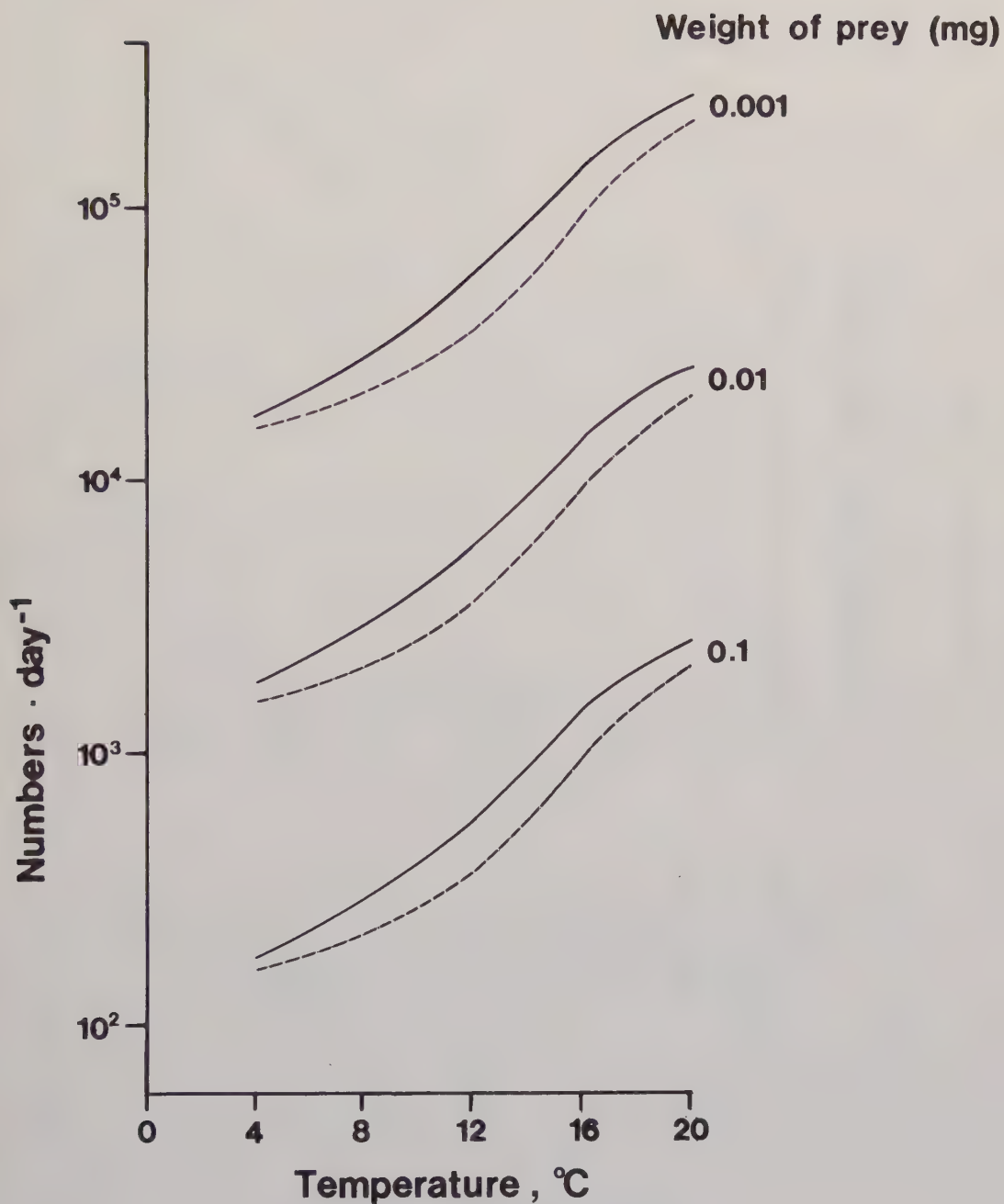


Fig. 3. Estimated number of prey of different organic dry weights which perch and roach of 10 g need to consume at different temperatures to attain maximum daily food consumption. Solid line = perch, broken line = roach.



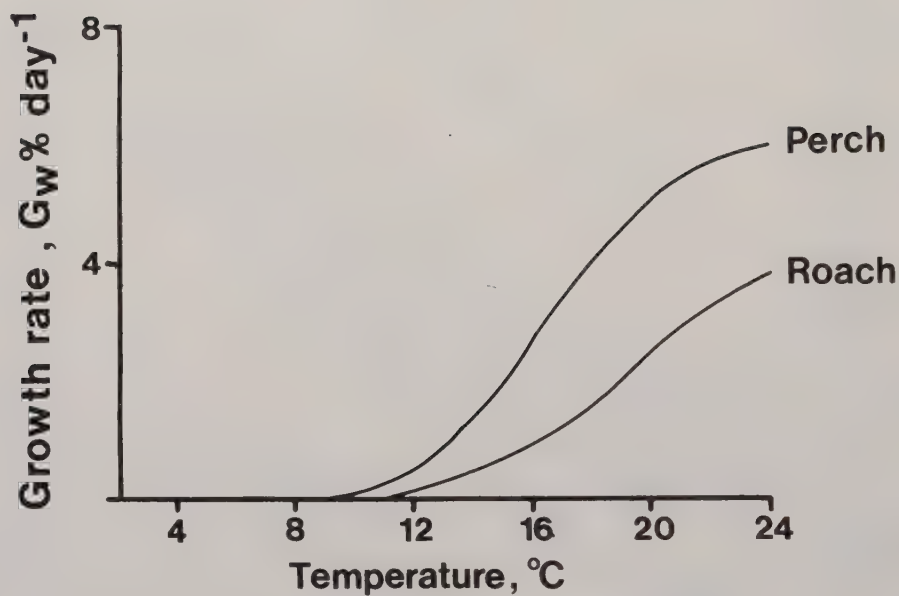


Fig. 4. Relationship between maximum growth rate and temperature in the range 4-24 °C for perch and roach of 10 g, fed maximisations of the diptera larvae, Chaoborus.

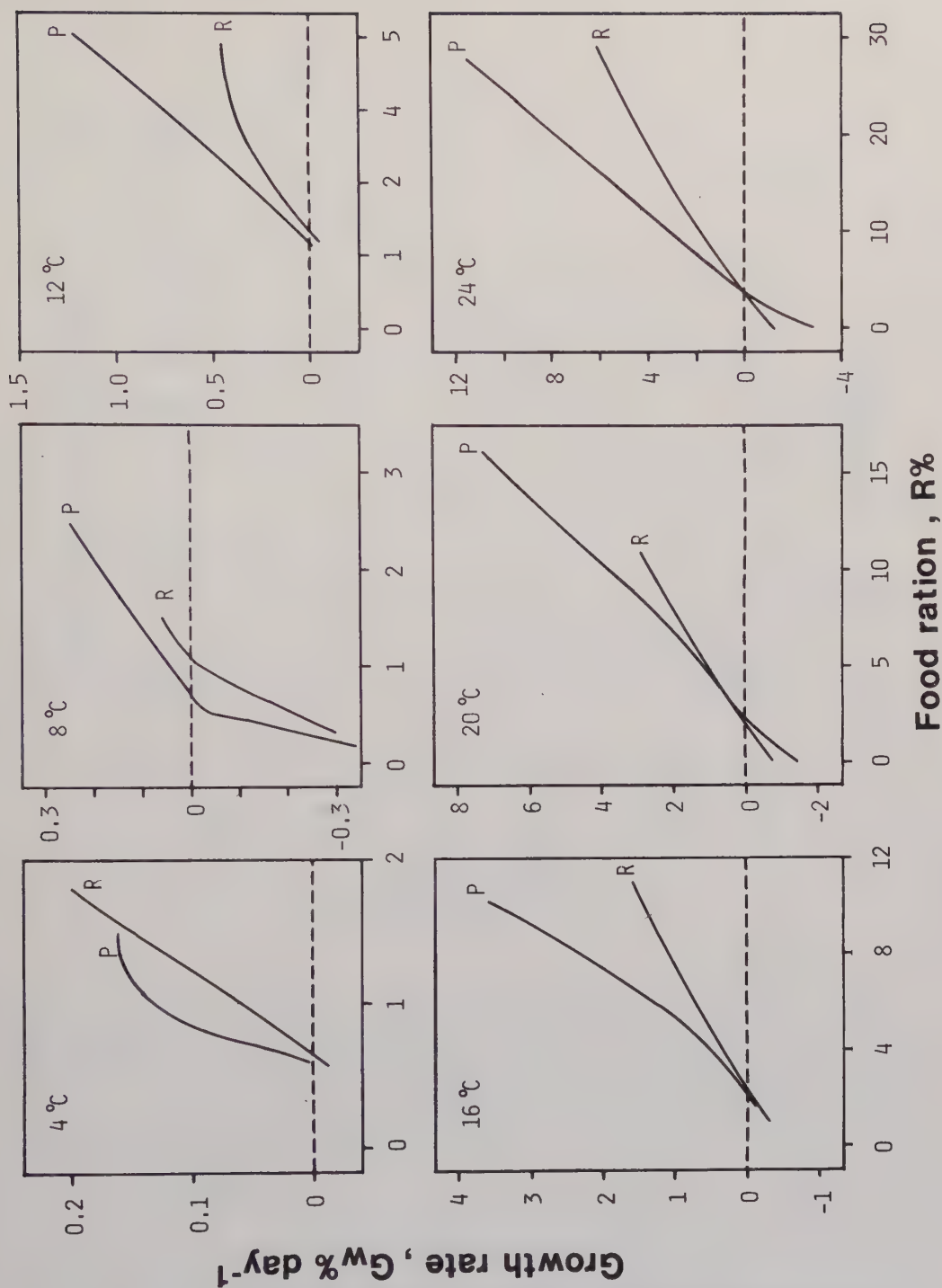


Fig. 5. Relationship, at different temperatures, between ration-size and growth rate for perch and roach weighing approximately 2 g. P = perch, R = roach. Note the different scales on the axes.

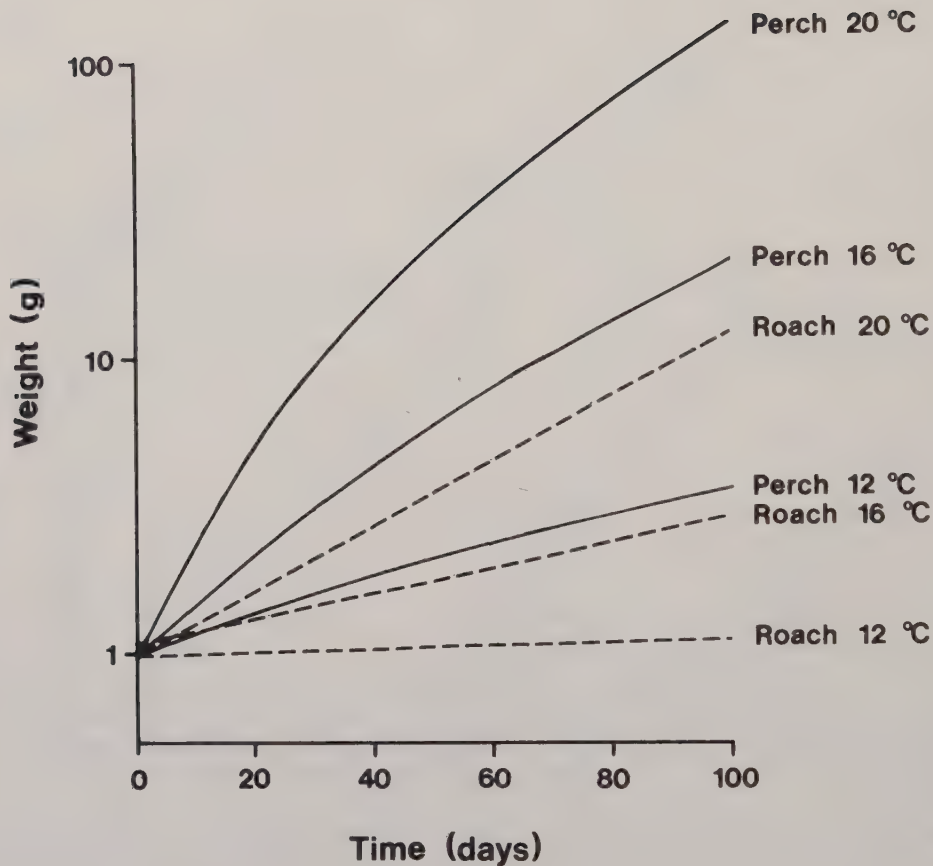


Fig. 6. Calculated theoretical maximum weight-increase during a 100-day period, at different temperatures, for perch and roach with initial weights of 1 g.

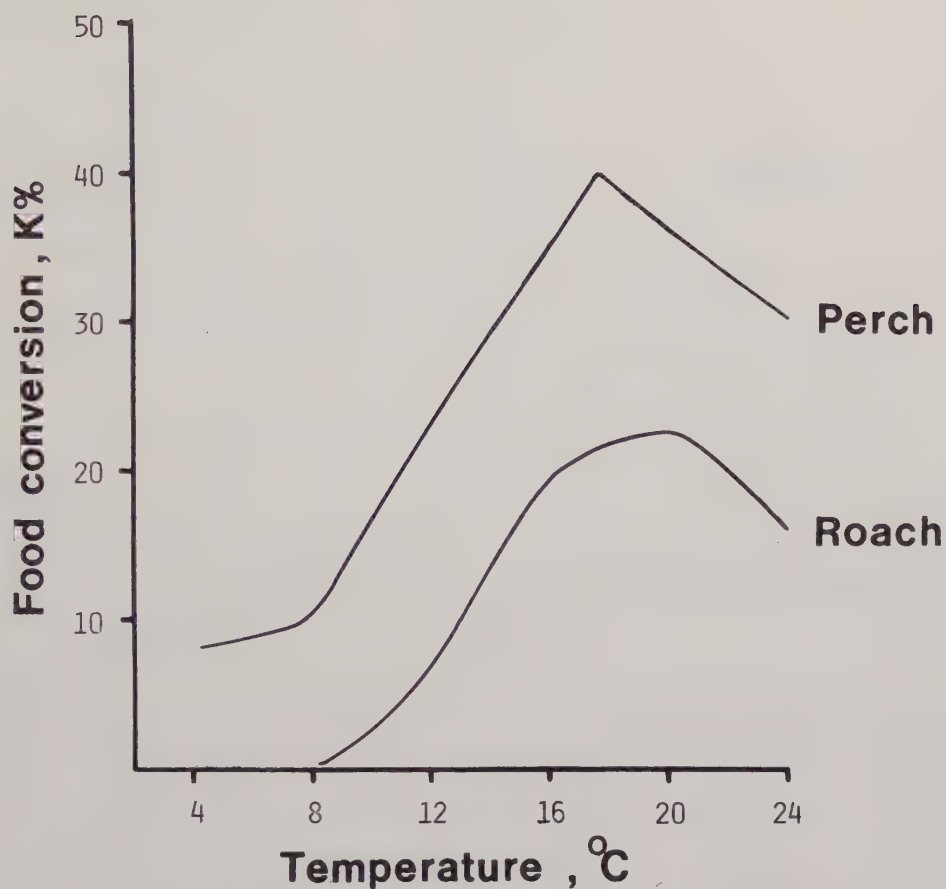


Fig. 7. Relationship between food conversion efficiency and temperature in the range 4-24 °C for perch and roach weighing 10 g and fed maximum rations of the diptera larvae, Chaoborus.

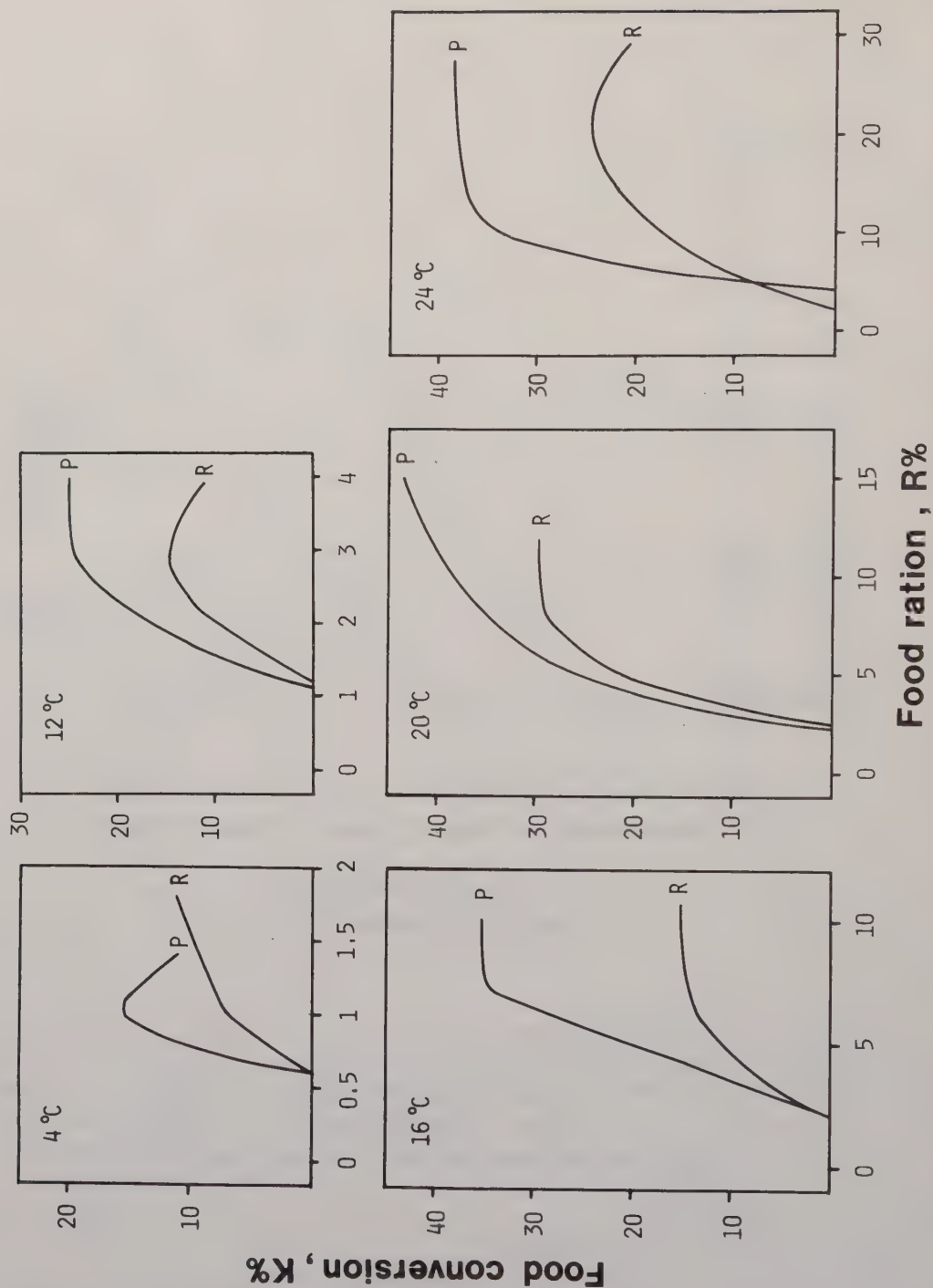


Fig. 8. Relationship, at different temperatures, between food conversion efficiency and ration-size for perch and roach weighing approximately 2 g. P = perch, R = roach. Note the different scales on the axes.



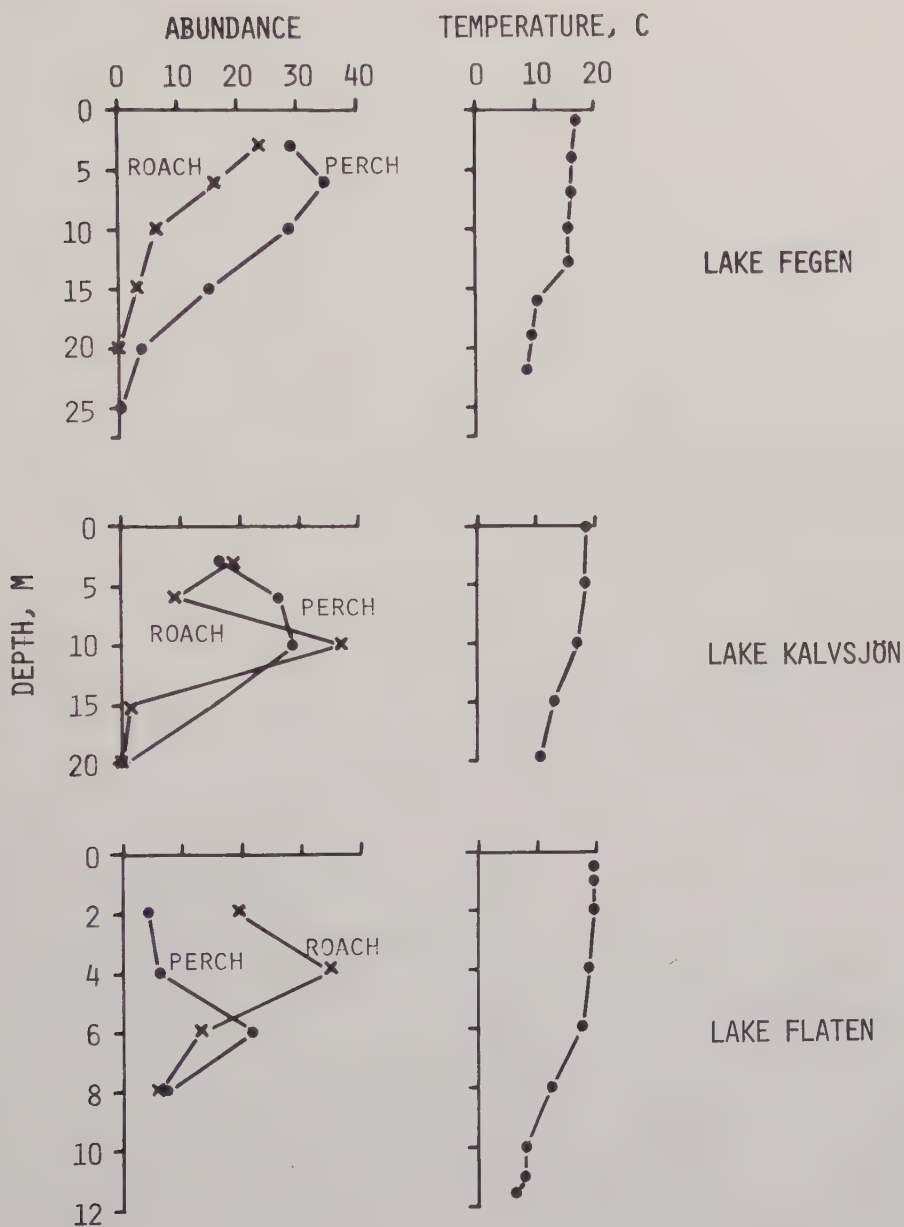


Fig. 9. Vertical distribution of perch and roach in three temperature-stratified lakes in Sweden. Number of fish caught per gill-net and day is used as a relative measure of abundance.



THE UTILIZATION OF PLANT MATERIAL FOR METABOLISM  
AND GROWTH BY ROACH (*Rutilus rutilus*)

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## SUMMARY

In laboratory experiments, roach consumed large amounts of the green algae Spirogyra, Enteromorpha and Meugeotia; the macrophyte Lemna minor; the blue-green alga Aphanizomenon flos-aquae and fresh detritus. Only L. minor and the blue-green alga could be utilized for growth and metabolism because roach cannot efficiently digest hard plant material with cellulose-rich cell walls. The growth rate on maximum rations of blue-green algae was  $0.9\%$  day<sup>-1</sup> and on a pure animal diet  $2.5\%$  day<sup>-1</sup>. A restricted ration of animal food supported by excess supply of blue-green algae resulted in a growth rate almost as high as on the maximum ration of animal food. A flexible feeding strategy and the ability to optimize food intake by combining a plant and animal diet, favours roach in food competition with more carnivorous fish species. This is one reason why roach dominate in many lakes.

## INTRODUCTION

Roach (Rutilus rutilus L.) is an omnivorous fish with a broad food spectrum. Their diet is often dominated by plant material such as macrophytes including Characeae, filamentous algae, decayed plants and detritus (Otterström 1931, Kempe 1962, Hellawell 1972, Mann et al. 1970, Ali 1973, Rachunas 1973, Prejs and Jackowska 1978, Preys 1978, Niederholzer and Hofer 1980, Linfield 1980). Planctonic algae are consumed to a small extent, mainly by juvenile individuals. The macrophytes consumed are species with small, soft parts e.g. Elodea canadensis, Ceratophyllum demersum, Lemna and Potamogeton species. In habitats where planctonic crustaceans or small benthic animals are abundant, they are preferred. Plant material seems to be a second class food, mainly consumed when there is shortage of food of animal origin (Lyagina 1972).

The use of plant material by herbivorous fish in laboratory experiments, has most frequently been estimated as assimilation efficiency (e.g. Sorokin 1968, Moriarty and Moriarty 1973, Dyke and Sutton 1977, Gunn et al. 1977, Bowen 1981) and few studies have shown whether plant material is enough to cover metabolic demand or is sufficient for growth (e.g. Kitchell and Windell 1970, Mathavan et al. 1976).

Although consumption of vegetable food is well documented,

knowledge of its nutritive value for roach is insufficient. The purpose of this work is to estimate to what extent different plants and detritus are used by roach for growth and metabolism.

## METHODS

The roach used in the experiments were taken from a stream, Hölje å, in Scania southern Sweden. They were acclimatized to experimental conditions for two weeks before the start of the experiments. During this time they were fed with the cladoceran Daphnia magna.

The fish were randomly divided into groups of six individuals. Each group was kept in a separate aquarium with a volume of 60 liters. The flow of water through the aquaria was constant and the retention time was 1.5 hours. The aquaria made up a semi-circulating system of 700 liters with a fresh water renewal time of 8 hours. Water leaving an aquarium was filtered and aerated before being recirculated. The temperature was kept at  $20 \pm 0.2$  °C, with a light regime of 18 hours light and 6 hours darkness.

After acclimatization, the fish were starved for one day before starting the experiments, to evacuate the gut. At the start of the experiments the roach were anaesthetized with MS 222 blotted on soft wet paper, and weighed to the nearest 0.01 g. Weights ranged from 2.3 to 10.9 g.

Eight different types of food and two combinations of food were tested. Each group was fed with a defined sort of food for eight days. One group was kept without food.

At the end of the experiments the fish were weighed in the same way as at the start. They were then killed and their gut content was removed, weighed to the nearest 0.01 g, and the colour and structure was compared to that of unconsumed food. The weight of the gut content was subtracted from the final total weight of the fish before calculating the specific growth rate according to:

$$G_w \% = \frac{\ln w_2 - \ln w_1}{t} \times 100$$

where  $G_w$  % is specific growth rate,  $t$  is duration of the experiment in days, and  $w_1$  and  $w_2$  is wet weight of the fish at the start and end of an experiment.

To check whether the body composition differed between groups treated in different ways, percentage dry weight content was calcu-



lated after drying the fish to a constant weight at 65 °C.

Starving results in a reduction of dry weight content when fat reserves are metabolised. It was assumed that if some kind of plant material could not be used for growth, it might be used to build up fat reserves. This might influence the growth rate and weight to a small degree, but could be monitored by assessing the dry weight content.

Three kinds of vegetable food material were tested: filamentous green algae (Spirogyra sp., Mougeotia sp. and Enteromorpha sp.), planktonic blue-green algae (Aphanizomenon flos-aque) and one macrophyte (Lemna minor). The plant material was carefully washed and rinsed to remove animals and epiphytes. A. flos-aque frequently forms bundles, which makes it easy to sample and separate from other organisms. Subsamples of the different foods were examined under a microscope and it was ascertained that the amount of contamination was insignificant. Filamentous algae were cut to about 5 mm-long pieces before being fed to the fish. The nutritive value of fresh and old algal detritus were tested. Old detritus was taken from a depth of 3 m with a core sampler from the centre of an eutrophic lake, Sövdeborgssjön, in southern Sweden. The upper 5 cm of the detritus core was removed and the material from 5 to 20 cm depth was used in the experiments. Fresh algal detritus was taken from the same lake. A net was placed in the pelagic zone of the lake for 2 months and the deposits on it were sampled. The detritus was sifted through a net with a mesh size of 0.5 mm to remove chironomids and other animals. Microscopic examination of the detritus revealed that it was mainly of algal origin. The fresh detritus contained a few living diatoms, but there were no living cells in the old detritus.

Fish fed with plants and detritus always had an access of food. In two experiments the fish were fed a combined plant-animal diet to determine whether use of plant material was influenced by the presence of higher quality protein. Two groups of fish received excess rations of plant food: one was fed Spirogyra, the other Aphanizomenon flos-aquae, and both received Daphnia magna equal to 55 % of their weight per day. Transformed to dry weight values, this equals approximately 8.8 % of their weight per day and corresponds to a bit less than half the maximum daily food consumption by roach fed purely with animal food (Lessmark 1983c). One group got no plant material besides Daphnia in the above amount.

Statistical tests on growth rate mean values were calculated by

an analysis of variance.

## RESULTS

### Growth rates

The growth rates ( $G_w\%$ ) of fish fed with filamentous green algae were not significantly different from the starving fish (Table 1,2). The mean value of  $G_w\%$  for fish fed with *Enteromorpha* was less than for starving fish, but the difference was not statistically significant. Fresh detritus appeared to be better quality food than old detritus, since weight loss of fish feeding on fresh detritus was less than for fish feeding on old detritus or for starving fish. Growth rates were however not significantly different. Filamentous green algae and detritus can be considered food with poor nutritive value and cannot be utilized for growth or to cover the metabolic requirement.

Lemna minor had some nutritive value and could be used to cover almost the entire metabolic requirement. Fish fed with the blue-green Aphanizomenon flos-aquae increased in weight. The quality of this material was much better for growth than any other food tested, excepting Daphnia. A mixture of animal food and Spirogyra, did not result in significantly better growth than a pure animal food diet of the same quantity. The addition of Aphanizomenon to the Daphnia diet increased the growth rate significantly.

Figure 1 shows the growth rate of roach fed with different rations of a purely animal diet and the growth rate on the same rations of animal diet plus an excess supply of blue-green algae. Value for the growth rate on an animal diet are from Lessmark (1983c).

### Dry weight content

The dry weight content of the fish at the end of the experiments reflected their use of the different food stuffs. Fish fed with detritus had the highest values of dry weight content (Table 1). However, these figures cannot be compared to the others since the initial fish material was not different. Detritus experiments were run in October and all other experiments in June. The fat content and dry weight value of roach are generally higher in autumn than in summer. Sediment-fed fish probably had higher dry weight values than the others even at the start of the experiments.

The high dry weight values were not a result of consumption and conversion of detritus into body fat since old detritus was not consumed.

In the experiments run simultaneously in June with fish taken from the same pool, it is assumed that the dry weight values of the different fish groups were equal at the beginning of the experiments. Fish fed with filamentous green algae and Lemna had lower dry weight content than those fed with blue-green algae or Daphnia (Table 1). These differences are probably due to starving and a reduction of the fat reserves of weight-losing fish. Differences in growth rates would therefore have been greater between fish with negative and those with positive weight change, if it had been calculated from energy values.

### Consumption and digestion

The fullness of the guts showed that all the kinds of food offered to the fish were consumed, excepting for old detritus (Table 1). Fish fed with Spirogyra, Mougeotia, Enteromorpha, Lemna and fresh detritus had well-filled guts, the weights of the contents varying from 1.1 % to 3.2 % of the body weight. These foodstuffs were the same colour and structure in the posterior and anterior parts of the gut. The only difference from fresh material was that Lemna plants had been mechanically splintered, and that blue-green algae had lost its structure and colour, turning dark brown like algal detritus. No undigested Daphnia remained in the gut of any of the fish as they had been fed their last daily ration of Daphnia 24 hours before the experiments ended.

### DISCUSSION

#### Use and digestion of plants

To have any nutritive value food material must have a chemical composition valuable to the consumer. Growth of fish depends on e.g. the proteins of certain amino acids (Covey and Sargent 1979). The consumer must also have an alimentary canal that can digest the food (Fänge and Grove 1979). Cells must be broken up and decomposed by enzymes. Use of a specific kind of food depends thus on its quality and digestability.

The usability of the various foodstuffs in this study depended a great deal on the cell-wall structure of the food and its digesta-

bility. Protein content does not explain the big differences in growth rates. Consumption of green algae and Lemna, which have a rigid cell-wall containing cellulose, resulted in a negative weight change. Blue-green algae and daphnids, which do not have a cell wall build up of cellulose, were successfully used for growth. Roach and other vertebrates do not produce the enzyme cellulase, which chemically breaks down the cell wall in plants. Slight cellulase activity was noted in the intestines of roach (Prejs and Blaszczyk 1977) and many other fish (Lindsay and Harris 1980) but this probably emanates from the ingestion of invertebrates containing cellulase. Roach lack the enzymes which can break up the cell wall, digest the cellulose and make assimilation possible. Other carbohydrates were, however, found in most investigated fish species (Kapoor et al. 1975). An ability to break up the cell walls and expose the cell contents to digestive enzymes seems to be important if plants are to be used by roach. This breaking down must be done by means other than the use of enzymes. There is no evidence that fish have an intestinal fauna like ruminants, which can be helpful for digestion.

When the experiments were planned, one hypothesis was that animal food contains enzymes which contribute to the digestion of plants. Another, was that plants lack some essential substance for fish growth, such as some amino acids, so that if the diet was supplemented by animal protein, algae could be used to improve fish growth. Both these hypotheses were later rejected.

Lobel (1981) pointed out two ways that herbivorous fish break up the cell walls of plants: acidolysis and mechanical fragmentation. Based on their morphological adaptations to digest plants, Lobel (op cit.) classified herbivorous reef fish in three categories. One group had thin-walled, soft stomachs with acid secretion and pH about 2-4, and the cells were chemically broken up. The other two groups had neutral pH in the intestines and plant cells were broken up mechanically. One group had gizzard-like, thick-walled stomachs and food was triturated, while the other group had a pharyngeal mill for breaking up cells. Roach most resembles this last group having no acid secretion intestinal, pH ranging from 6 to 8 (Barrington 1957) and lacking the stomach type for trituration. The only way to break up cellulose-rich cell-walls is mechanically, using the pharyngeal teeth. This is directly related to assimilation efficiency, so that when the proportion of broken cells increases, digestability also increases.



Hicklings (1966) study of the feeding process of the white amur or grass carp (Ctenopharyngodon idella) confirms this. Grass carp also have pharyngeal teeth, enzymes and an intestine very similar to roach. Alteration of food in the intestine was very similar to what I observed. Hickling (op. cit.) stated that when suitable food was available, feeding was continuous and the gut appeared filled throughout its length with green material. Large pieces of leaf appeared to pass through gut unaffected. Only those cells which were rasped or cut appeared to be digested. Approximately 50 % of the food was assimilated. In a feeding experiment, grass carp assimilated 61 % of the energy and 80 % of the crude protein from Lemna sp. (Dyke and Sutton 1977).

The ability to mechanically break up plant cells must also depend on their structure, as it is reasonable to assume that hard and tough plants are harder to grind than soft ones. This is probably the reason for the slight difference in the digestion of green algae and Lemna by roach. The green algae in the posterior and anterior parts of the intestine looked like fresh algae. Lemna, which is softer than the filamentous algae, preserved its green colour in the intestine but had been cut up into smaller pieces. It had some nutritive value.

Since the fish consumed all the kinds of food available, except old detritus, food selection cannot explain the differences in growth rates.

The chemical composition of food, and especially the protein content, is one of the factors determining its nutritional value for growth. Assimilation efficiency of proteins is generally higher than for total organic matter (Dyke and Sutton 1977, Bowen 1981). Of the used foodstuffs in this study, daphnids and blue-green algae had the highest protein content (Table 3). These food items also resulted in the highest growth rates. However, growth rate was not only determined by protein content of the food. Green algae, which contains about one third of the protein in blue-green algae, was not used at all. Neither was detritus, with a protein content of 15-21 %. The quality of the protein is also an important factor for growth, as high protein content does not necessarily result in good growth. Chemical composition and digestability co-operate and determine the nutritive value of different kinds of food.

The nutritive value of detritus depends on its origin and degree of decomposition because the chemical composition changes during decomposition. Since fresh blue-green algae has a high nutritive



value, blue-green algal detritus probably also has a high nutritive value for roach, depending on how fresh the detritus is. According to Bengtsson et al. (1977), seston had double the amount of amino acids found in sediment, and Ulén (1977) found that seston had twice as much protein than sedimenting, partly recycled material collected in sediment traps.

The roach made slightly better use of fresh detritus than of old detritus, but this was not statistically significant. Roach can probably use better quality detritus than that used in this study by feeding more selectively on the sediment like striped mullet, Mugil cephalus (Odum 1968). Mann et al. (1970) estimated the assimilation of organic detritus by roach and concluded that roach were very selective in their feeding; samples of detritus similar to that eaten by the fish could not be collected in the field. Sorokin (1968) stated that both fresh blue-green algae and blue-green algal detritus had a high nutritive value for roach.

Despite this there are only a few reports from field studies on blue-green algae in the guts of roach. On the other hand, detritus in the guts has been frequently noted. Since the blue-green algae in the laboratory experiments changed colour and looked like detritus in the guts it is possible that gut content classified as detritus by many authors may have been blue-green algae or blue-green algal detritus.

It is not known why roach consume food like green algae and detritus, which does not give any net energy gain. Hofer and Niederholzer (1980) observed that on a diet of filamentous algae, weight loss of rudd (Scardinius erythrophthalmus) was just slightly less than that of starving fish. Roach feeding on filamentous algae for three weeks in laboratory experiments showed signs of hunger metabolism with changes in the free amino acid pools in the tissue (Knapp and Wieser 1981). Consumption of Spirogyra, Mougeotia and Lemna by roach has been reported from field studies. It is possible that these food-types are consumed to satisfy vitamin or mineral needs. The only present explanation is that roach cannot distinguish plants of different nutritive value.

Efficiency in digesting plant material is generally estimated as assimilation and depends very much on the fish species and the kind of food. Species with strong acid secretion seem to assimilate green algae much better than those with a more neutral pH in the intestine. Sarotherodon mossambica, with a pH of less than 1.5 in the gut (Bowen 1981), assimilated 78.5 % of the carbon in the green al-

gae, Spirogyra (Mathavan et al. 1976), but just 23 % of the total carbon in the same plant was assimilated by Ichталurus nebolosus (Gunn et al. 1977), that has a pH in the stomach of 2-4 (Page et al. 1976). On the other hand, I. nebolosus assimilated 67 % of the carbon in the blue-green algae Anabena flos-aquae (Gunn et al., op. cit.).

In my study, Spirogyra had no nutritive value for roach with intestinal pH in the range 6-8 (Barrington 1957). Sorokin (1968) found that roach assimilated blue-green algae almost as efficiently as animal food and about five times more efficiently than green algae. Moriarty (1973) was convinced that low pH in the gut was the reason why Tilapia nilotica successfully assimilated and grew on a diet of blue-green algae. Results from my study and Sorokin's (op. cit.) indicate that blue-green algae can also be used successfully by fish, like roach, which have no acid secretion and neutral pH in the gut, and by fish with a weak acid secretion, like I. nebolosus. However, green algae seem to be efficiently digested only by fish with very strong acid secretion in the gut.

#### Optimizing food intake

The addition of blue-green algae to a sub-optimal ration of animal food increased the growth rate from 1.6 % day<sup>-1</sup> to 2 % day<sup>-1</sup>. The growth rate on an excess ration of only blue-green algae was 0.9 % day<sup>-1</sup>, and on a pure animal diet, 2.5 % day<sup>-1</sup>. An animal-plant combination diet results in a slightly lower growth rate than that on a pure animal diet.

Depending on the availability of animal and plant food, roach can optimize its food intake for growth. If the supply of animal food is limited but the vegetable food supply is unlimited, roach may still consume maximum rations. Depending on how much energy the fish has to spend for catching animal prey, a switch to a plant diet or a mixed diet of plant and animal food, may be more favourable. The combination optimal for growth would depend on the abundance of prey and blue-green algae. The frequency of plants in the diet of roach has been reported to increase when animal food is less abundant (Lyagina 1972).

The effects of plant consumption on interspecific competition and abundance.

In lakes undergoing eutrophication the biomass of roach and other cyprinids increases more than that of percids and coregonids (Leach et al. 1977). Roach is generally more dominant in eutrophic lakes than in oligotrophic lakes, and blue-green algae often dominates phytoplankton communities in eutrophic lakes more than in oligotrophic lakes. Since blue-green algae can be used by roach, the total food basis increases and this may be one explanation for the observed changes in the fish communities in lakes undergoing eutrophication.

Competition for food is often severe between different fish species. As roach may switch to a more plant-dominated diet when there is a lack of animal food, they can continue to grow when more carnivorous competitors can no longer grow. Thus, roach has the advantage over more carnivorous fish in that it does not have to focus all its foraging effort on animal prey. This flexible feeding strategy has high competitive value.

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Table 1. Specific growth rate, dry weight content and food content in the gut of roach (*Rutilus rutilus*) fed with different kinds of food at 20 °C. Food of animal origin was always restricted but food of plant origin was in excess.

\$ = values not comparable to other values because of differences at the start of the experiment.

| Food material                                             | Specific growth rate<br>$G_w \pm 95\% \text{ C.L.}$ | Dry weight content of fish<br>% of wet weight $\pm 95\% \text{ C.L.}$ | Food content in the gut<br>% of fish weight $\pm 95\% \text{ C.L.}$ |
|-----------------------------------------------------------|-----------------------------------------------------|-----------------------------------------------------------------------|---------------------------------------------------------------------|
| NO FOOD:                                                  | -0.72 $\pm$ 0.09                                    | 20.2 $\pm$ 1.2                                                        | 0.0                                                                 |
| FILAMENTOUS GREEN ALGAE:                                  |                                                     |                                                                       |                                                                     |
| <u>Spirogyra</u>                                          | -0.64 $\pm$ 0.33                                    | 20.8 $\pm$ 1.6                                                        | 3.2 $\pm$ 1.2                                                       |
| <u>Mougeotia</u>                                          | -0.67 $\pm$ 0.13                                    | 20.1 $\pm$ 1.3                                                        | 1.4 $\pm$ 0.3                                                       |
| <u>Enteromorpha</u>                                       | -0.94 $\pm$ 0.49                                    | 20.2 $\pm$ 1.7                                                        | 2.0 $\pm$ 1.5                                                       |
| MACROPHYTE:                                               |                                                     |                                                                       |                                                                     |
| <u>Lemna minor</u>                                        | -0.22 $\pm$ 0.12                                    | 20.2 $\pm$ 0.6                                                        | 1.8 $\pm$ 1.5                                                       |
| DETRITUS:                                                 |                                                     |                                                                       |                                                                     |
| Old                                                       | -0.74 $\pm$ 0.11                                    | 22.9\$ $\pm$ 1.6                                                      | 0.0 $\pm$ 0.0                                                       |
| Fresh                                                     | -0.47 $\pm$ 0.17                                    | 22.0\$ $\pm$ 1.7                                                      | 1.1 $\pm$ 1.0                                                       |
| BLUE-GREEN ALGAE:                                         |                                                     |                                                                       |                                                                     |
| <u>Aphanizomenon flos-aquae</u>                           | +0.90 $\pm$ 0.33                                    | 22.0 $\pm$ 1.0                                                        | 0.3 $\pm$ 0.2                                                       |
| ANIMAL FOOD:                                              |                                                     |                                                                       |                                                                     |
| <u>Daphnia</u> 55 % of fish body weight day <sup>-1</sup> | +1.64 $\pm$ 0.55                                    | 21.9 $\pm$ 2.2                                                        | 0.0                                                                 |
| <u>Daphnia</u> 55 % + <u>Spirogyra</u>                    | +1.81 $\pm$ 0.55                                    | 21.9 $\pm$ 2.0                                                        | 0.0 $\pm$ 0.1                                                       |
| <u>Daphnia</u> 55 % + <u>Aphanizom.</u>                   | +2.03 $\pm$ 0.37                                    | 21.8 $\pm$ 0.6                                                        | 1.2 $\pm$ 0.8                                                       |

|              |                  | F-value  |     | t-value |     |
|--------------|------------------|----------|-----|---------|-----|
| No food      | - Spirogyra      | .1502    | ns  | .3875   | ns  |
|              | - Mougeotia      | .0679    | ns  | .2606   | ns  |
|              | - Enteromorpha   | 1.3721   | ns  | 1.1714  | ns  |
|              | - Lemna minor    | 6.8264   | +   | 2.6127  | +   |
|              | - Detritus old   | .0184    | ns  | .1358   | ns  |
|              | - Detritus fresh | 1.6038   | ns  | 1.2664  | ns  |
|              | - Aphanizomenon  | 71.2215  | +++ | 8.4393  | +++ |
|              | - Daphnia        | 151.0241 | +++ | 12.2892 | +++ |
|              | - Daphn.+Spir.   | 174.2941 | +++ | 13.2020 | +++ |
|              | - Daphn.+Apha.   | 205.0218 | +++ | 14.3186 | +++ |
| Daphnia      | - Daphn.+Spir.   | 0.8333   | ns  | 0.9129  | ns  |
|              | - Daphn.+Apha.   | 4.1185   | ns  | 2.0294  | +   |
| Daphnia      | - Aphanizomenon  | 14.8217  | +++ | 3.8499  | +++ |
| Lemna        | - Aphanizomenon  | 33.9487  | +++ | 5.8266  | +++ |
| Detritus old | - Detritus fresh | 1.9662   | ns  | 1.4022  | ns  |

Table 2. ANOVA test for the mean growth rates of roach fed with different foods. ns= difference not significant at  $p < 0.05$  level. + =  $p < 0.05$ , +++ =  $p < .001$ .

Table 3. Protein content of the food material used in the experiments.

| Food stuff       | Protein content<br>% of dry weight | Source                               |
|------------------|------------------------------------|--------------------------------------|
| Green algae      | 11-28                              | Collyer and Fogg 1955                |
| Blue-green algae | 41-56                              | "                                    |
| <u>Lemna</u>     | 34.8                               | Dyke and Sutton 1977                 |
| <u>Daphnia</u>   | 60                                 | Vijverberg and Frank 1976            |
| Detritus fresh   | 21                                 | Calculated from<br>Kjeldahl-nitrogen |
| Detritus old     | 15                                 | value                                |

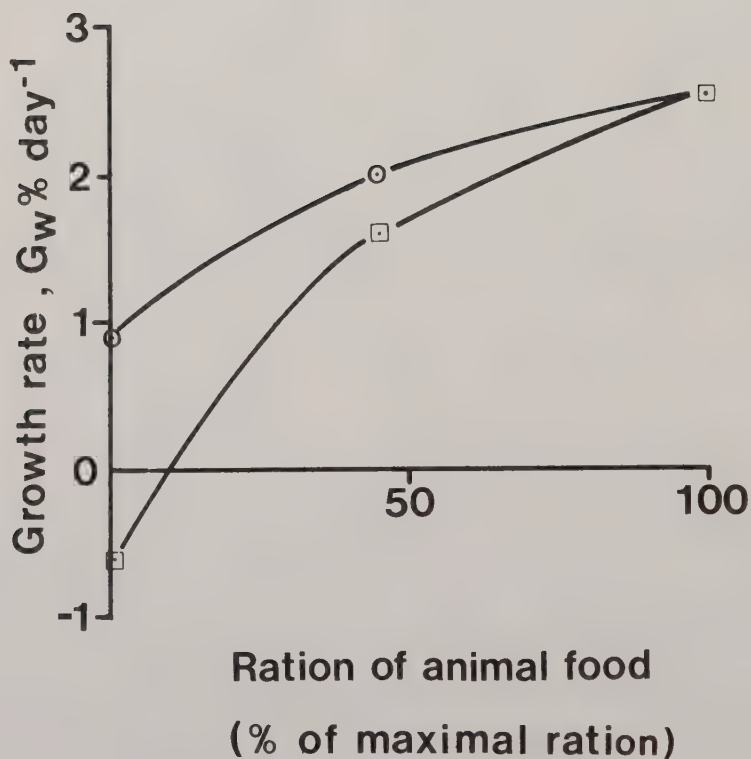


Figure 1. Growth rate at 20 °C of roach given different rations of animal food (lower line) , and those given the same rations of animal food plus excess rations of blue-green algae (*Aphanizomenon flos-aquae*) (upper line).



SELECTIVE ZOOPLANKTON PREDATION BY PERCH AND ROACH  
Experimental studies on interspecific competition

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## SUMMARY

In laboratory experiments, perch and roach were size-selective when offered zooplankton of different sizes. Roach was a more adept predator on small zooplankton than perch. The minimum prey size for 7-8 cm long fish was 0.5 mm for perch and 0.3 mm for roach. This difference magnified as the size of the fish increased. This is explained by differences between the two species as regards sight, adaptness at detecting prey, foraging behaviour and energy expenditure per prey. Roach had difficulties capturing fast-moving copepods and elected immobile and slow-moving prey. Roach can be described as a cropper, whereas perch behaved more like a hunter, consuming more mobile prey. Result from the laboratory studies agreed with field studies. As roach is better able to make use of small zooplankton throughout its lifespan, a larger proportion of the zooplankton community is available to it as food compared with that available to perch. Roach disfavours perch by reducing the size of zooplankton so much that they only can be used as food by the smallest perch. This is one of the reasons why roach is dominant in many lakes and why its biomass is much higher than that of perch. In lakes where there is no roach, zooplankton is generally larger, and perch is more planktivorous than in lakes where the two species live together.

## 1. INTRODUCTION

Interest has been increasingly focused on how fish select their prey since it has been demonstrated that fish predation strongly influences zooplankton communities. The species composition and abundance of zooplankton in lakes are affected by fish density (Hrbacek 1958, Hrbacek et al. 1961) and variety of fish species (Brooks and Dodson 1965, Nilsson and Pejler 1973, Stenson 1979). Early studies by Ivlev (1961) and later papers on prey selection (i.e. Mellors 1975, Janssen 1976, Confer et al. 1978, Eggers 1978, O'Brien 1979, Vinyard 1980) describe how predation takes place, what species of prey is preferred and how selection can be explained by factors such as the size, visibility and mobility of zooplankton (see Egger's review 1978). Some researchers used theories of optimal foraging to explain preference patterns (i.e. Werner and Hall 1974, Krebs 1978).

Studies have concentrated more on how fish influence zooplankton communities, and less on how these communities influence fish popu-

lations. Svärdson (1976) and Nilsson (1978) pointed out that adeptness of catching zooplankton was significant for interspecific competition between fish. The dominance of some fish species seemed to correlate with their adaptness at catching small zooplankton. This was first proved in lakes dominated by one or more of the following fish species: brown trout (Salmo trutta), arctic charr (Salvelinus alpinus) and whitefish (Coregonus sp.). In lakes where brown trout had been dominant, this species had decreased after the introduction and expansion of the more adept zooplankton predator, arctic charr. This was accompanied by a continual decrease in the size of zooplankton. Large, colourful species of crustaceans such as Daphnia longispina and Heterocope saliens dominated in lakes where the only fish was brown trout (Nilsson and Pejler 1973). In lakes containing arctic charr, D. longispina was replaced by the smaller species D. galeata. Similarly, the biomass of arctic charr decreased after the introduction of whitefish, and in lakes containing whitefish, Heterocope saliens was replaced by H. appendiculata, and the small species D. cristata became the dominant daphnia.

Perch (Perca fluviatilis) and roach (Rutilus rutilus) are common fish species, often found coexisting in Scandinavian lakes. The young of both species prey mainly on zooplankton. The aim of this investigation is to study selective predation on zooplankton crustaceans by perch and roach and to analyze how this influences dominance relations and interspecific competition between the two species. My hypothesis is that the species better able to catch smaller zooplankton should dominate in lakes where the two species live sympatrically.

## 2. METHODS

Thirteen experiments were done in rectangular glass aquaria of 100 l water at  $20 \pm 2$  °C. The fish were acclimatized to experimental conditions for at least 7 days before the start. They were fed daphnids or the diptera larvae, Chaoborus sp., and were starved one or two days before the experiments started in order to evacuate the guts and to standardize hunger.

The perch in experiments 1-12 had a mean total length of 71 mm ( $SD \pm 6$  mm) and the roach, 80 mm ( $SD \pm 11$  mm).

In experiments 1-9, the fish were offered zooplankton prey samples and prey selection was studied. The prey samples were taken from 9 different lakes and ponds. To simulate lake conditions, zooplankton from 100 l water was collected in a net and concentrated

in 1 l water in experiments 1-7 and 9. For experiment 8, zooplankton was collected by dragging a net through open water. Subsamples were taken for analyses of species and size.

In each of the tests, 4 or 5 perch and the same number of roach were used. They were offered prey samples of planktonic crustaceans and were allowed to feed for 20 minutes. Then they were killed and preserved in ethanol. The exposure time was long enough for the fish to consume enough prey samples for analyses, but short enough not to glut the fish and to ensure that the variety of prey samples available for consumption was only moderately affected.

The zooplankton in prey samples and fish stomachs were identified and measured in an Utermöhl microscope, according to figure 1. The electivity index (E) for different kinds of prey was calculated using Ivlevs equation (Ivlev 1961):

$$E = \frac{r - p}{r + p}$$

where r is the relative value of any ingredient in the predators ration, and p is the relative value of some ingredient in the environmental food complex. A positive E value for a prey species indicates that it has been actively selected.

Experiment number 10 was performed to compliment the results obtained in experiments 1-9. The purpose was to establish wheather either of the fish species was more capable of detecting and catching smaller food items. In this experiment, Daphnia magna were divided into one group of small (1.04-1.39 mm long) and one group of big (2.52-3.35 mm) individuals, with 50 specimens in each group. A group of 5 perch and 5 roach of equal size (about 7 cm) was offered the daphnids one at a time, randomly chosen from the two size-groups, and I noted which fish species took the prey sample. This experiment was run at short intervals during a 10 hour period.

In experiment number 11, escape of daphnids and cyclopoid copepods was studied when attacked by a predator. A group of 5 perch and 5 roach were kept separately. Each group was fed with either one or a few daphnids or copepods. I offered ten individuals of each prey species to each individual fish and recorded how many times each prey was attacked before beeing consumed.

In experiment 12, I compared the rates of consumption of a uniform food-type for the two fish species. Twenty perch and the same number of roach were offered approximately 200 Chaoborus larvae for

20 minutes. After this time the fish were killed and the number of prey samples in the intestines was counted.

In experiment 13, I estimated the smallest prey-size consumed when no bigger prey was available, and noted the correlation with fish-size. Perch and roach of different size classes were kept separately in aquaria. Four groups of 4 perch with sizes  $61 \pm 2$  mm,  $78 \pm 3$  mm,  $115 \pm 3$  mm and  $153 \pm 6$  mm; and four groups of 4 roach with lengths  $74 \pm 2$  mm,  $87 \pm 1$  mm,  $118 \pm 3$  mm and  $156 \pm 3$  mm were tested. Each group was fed with zooplankton divided into size classes. The fish were first fed with a mixture of rotifers and ciliates  $0.12 \pm 0.06$  mm long, and watched for ten minutes to see wheather they started feeding. They were then fed with bigger prey samples of calanoid copepods,  $1.3 \pm 0.2$  mm long, and it was noted whether the fish started foraging. Following the same procedure, I offered the fish a mixture of cyclopoid copepods and daphnids  $1.8 \pm 0.2$  mm long and daphnids  $2.8 \pm 1.0$  mm long. The aquaria were then cleared of unconsumed prey and the test was repeated after two days. In this second test, the fish were first fed with rotifers  $0.16 \pm 0.04$  mm long, followed by cladocera, Chydorus sp.,  $0.29 \pm 0.06$  mm long, and finally with daphnids  $1.9 \pm 0.5$  mm long. Fresh prey samples were supplied every hour. To confirm the visual recordings, the fish were killed at the end of the experiment and their gut contents were examined.

### 3. RESULTS

#### 3.1. Prey selection: Species

##### 3.1.1. Perch

Perch was strongly selective for Leptodora kindtii when this species was present (Table 1, Figure 2). Calanoid copepods also had a high electivity index which was about the same as the index for Leptodora when the two species ocured simultaneously. When calanoid copepods and daphnids were present in the same experiment, daphnids were preferred when represented by Daphnia longispina (experiment 2) and calanoid copepods were preferred when daphnias were represented by the smaller species, D. cucullata (experiment 7). In these experiments, size was the determining factor and the largest samples were always preferred.

Small daphnids were preferred to cyclopoid copepods in experiments 5,7 and 8, but in experiments 1,3 and 4, copepods were preferred.



red. In experiments 1,3,4 and 5, there were less than 2 daphnids per litre, so I could not draw any conclusions about preference. In experiment 8, where the daphnids were bigger than the copepods, the daphnids were preferred. In experiment 7, where the daphnids were smaller, they were still preferred. I concluded that daphnids were preferred to cyclopoid copepods of the same size.

Few Bosmina and Chydorus were consumed. Chydorus occurred in experiments 1,3,4 and 6, but was only consumed in one case and then only one specimen per fish. Few Bosmina were consumed in the two experiments where they were present. Experiment 3 showed that Chydorus and Bosmina were elected to the same low degree. Copepod nauplii was present in seven experiments but was not consumed, despite an abundance of 6.6 individuals per litre in experiment 9, where there was also a deficiency of bigger zooplankton.

Thus the zooplankton in the experiments with perch rank according to the most preferred species: Leptodora kindtii, Daphnia longispina, calanoid copepods, D. cucullata, cyclopoid copepods, Bosmina and Chydorus, copepod nauplii.

### 3.1.2. Roach

The prey samples in the stomachs of roach were ground by the pharyngeal teeth and this made identification difficult. In experiments 1,3 and 8, the prey samples could be identified by their body parts, but in the other experiments the pieces were too small for identification. No food was consumed in experiment 9. The length of the prey samples in the stomachs could not be calculated. Figures were drawn assuming that composition was not size selective within a zooplankton species.

Roach had a strong preference for Leptodora kindtii (Table 2, Figure 2). Few copepods were consumed and then only in one experiment, where daphnids were scarce. Although I observed that the fish detected the copepods and attacked them, they generally failed to catch them because the copepods escaped by jumping away. Ehippia were strongly preferred. They were dark pigmented and were probably easy to detect. Daphnia was preferred to Bosmina and Chydorus and copepod nauplii was not consumed.

In the experiments with roach the most preferred zooplankton species ranked: Leptodora kindtii, ehippia, Daphnia, Bosmina, Chydorus, cyclopoid copepods and copepod nauplii.

### 3.2. Prey selection: size

#### 3.2.1. Perch

In all experiments perch strongly preferred the biggest samples of zooplankton ( $\chi^2$ -test;  $p < 0.001$ , Table 3). This was most obvious when Leptodora and calanoid copepods were present.

The mean size of daphnids consumed by perch was bigger than the mean size of the prey sample (Table 4), but the difference at a  $p < 0.05$  level (Mann-Whitney U-test) was significant in only one of three experiments. Perch did not have a similar preference for the bigger cyclopoid copepods (Table 5), and predation of copepods was not size selective within the size range used in these experiments. The snatchy movement of copepods might have made it easier for perch to detect them. This would diminish the importance of the size factor for detection. Daphnids, however, move more uniformly and their size seems to contribute most to their detection.

The smallest prey samples consumed by perch were about 0.4 mm long but only one such sample was consumed per fish. In the other experiments, only prey samples bigger than 0.5 mm were consumed and this can be concluded to be the lower prey size of perch of this size.

#### 3.2.2. Roach

Apart from copepods which roach had difficulties catching, size selective predation was evident in experiment 3 and 8 (Table 2, Figure 2). In experiment 1, size was not the main factor. Pigmentation was decisive and roach preferred the dark ephippia. Copepod nauplii were not consumed and the lower size limit for about 8 cm long fish was 0.3 mm.

### 3.3. Prey detection

Experiments 1-8 showed that roach was more adept at detecting small prey. This was confirmed in experiment 10. Most of the large (2.52-3.35 mm) daphnids were consumed by perch and most of the small (1.04-1.39 mm) daphnids were consumed by roach (Table 6,  $\chi^2$ -test,  $p < 0.001$ ).

### 3.4. Escape by prey

In experiment 11, it was clear that daphnids, attacked by either perch or roach, were struck at the first attack (Table 7). They did

not try to escape, as did the copepods. The escape attempts by copepods succeeded best when under attack by roach, which had to strike on average 3.7 times before the cyclopoid copepods were consumed. This is a minimum value, since many copepods escaped so adeptly that the observer could not catch sight of them after the first attack. These successful copepods were thus not included in the results. Perch generally struck the copepods at the first attack, averaging 1.2 attacks per prey.

### 3.5. Consumption rates

Figure 3 shows the relationships between consumption rate and prey abundance for perch in experiments 1-9. Prey abundance values do not include unconsumed items like copepod nauplii, ehippia, Bosmina and Chydorus. When big prey such as Leptodora was present perch strongly preferred them, so experiments with Leptodora were not included when the curve was fitted. The correlation between consumption rate and prey abundance was positive up to a prey density of about 50 individuals per litre. At higher prey densities the consumption rate was unaffected. Perch could eat a maximum prey samples per minute, irrespective of prey density. The minimum time for the detection, catching and handling of a prey sample was 6 seconds. Nothing was consumed when prey abundance was 2 or less per litre. In experiment 2 and 5, prey was equally abundant. Despite the fact that the daphnids and copepods in experiment 2 were much bigger than those in experiment 5 the consumption rate and handling time was about the same in both experiments.

As prey consumed by roach was ground up, consumption rates for roach could not be calculated in the same way as for perch. However, consumption rates can be compared to some extent. When the fish were fed with Chaoborus (experiment 12), perch consumed more prey than roach in the same time (Table 8). In experiment 8, both fish species consumed the same kind of food and also in this case perch had the highest consumption rate. In experiment 1 and 3, consumption rates cannot be compared since the two fish species preferred different types of prey and these were present in different amounts.

### 3.6. Correlation between fish size and the smallest prey consumed

As the size of the perch increased, the size of the smallest prey sample increased (Figure 4). The minimum size of prey samples

was not dependent on the size of the roach.

## 4. DISCUSSION

### 4.1. Feeding strategies

Anatomical factors determine the size of prey suitable for consumption, the upper limit depending on the width of the fish gape and pharynx. The minimum size of prey is determined by factors such as: sight and adeptness at detecting prey (Sbikin 1974); number of gill rakers and filtering capacity (Nikolski 1969); body shape, and fine locomotor response (Werner 1977, Krebs 1978) and other handling abilities. Predators may also neglect prey which has a low energy content or is difficult to handle in order to maximize food intake (Werner and Hall 1974, Krebs 1978).

In my experiments the size of the zooplankton offered was below the anatomical upper limit. The biggest prey samples were probably preferred because they were easier to detect and because their energy value was higher per prey sample. The distance at which a fish detect prey increases as the size of the prey increases (Confer et al. 1978), so that, compared to their abundance, proportionately more big prey is visible to the fish.

When different prey sizes were available to fish about 7 cm long, the smallest prey consumed was 0.3 mm for roach and 0.5 mm for perch. This difference magnified as the size of the fish increased. This might be due to the fact that fish optimize foraging by neglecting prey under a certain size for which the energy expenditure is too high compared to the energy intake. The energy cost for handling must be higher per prey for perch than for roach. This would explain the differences in the size of the prey consumed by the two species. Foraging roach move slowly and select slow-moving or immobile prey like ephippia, sometimes rejecting contaminating matter such as small, hard pieces of plant and faeces. When attacking, perch rush at the prey and the current caused by opening the mouth and opercula sweeps the prey into the mouth. Roach has a uniform, slow swimming speed, whereas perch swim quickly and spasmodically. This, and other behavioural qualities of perch, causes greater energy consumption per prey and is better adapted to bigger prey which attempts to escape. Thus, the feeding strategy of perch characterizes it as a hunter, while roach may be called a cropper. This explains the differing lower size-limits for the two species as regards profitable prey.



The lower size limit of prey for each species might also be determined by deftness at detecting small prey. The fish in these experiments, preyed on individuals and never filter feed, as does alewife (Alosa pseudoharengus) which uses both methods of feeding (Janssen 1976). Prey was evidently discovered by visual orientation, since both perch and roach stopped feeding in darkness.

As experiment 10 shows, roach was better able to detect small preys than perch. Perch did not purposefully neglect small prey because smaller prey was consumed in experiments 1-8 and 13.

Copepods were consumed by perch in abundance, but not by roach. This pattern was also observed in lakes where the food of young perch and roach was studied simultaneously (Ali 1973, Stenson 1979). In Lake Bolmen (Häggström and Malmqvist 1970), copepods were the dominating planktonic crustaceans and the dominating food for perch. Copepods were unimportant for roach, which fed on cladocerans. This was also the case in a bay of the Baltic (Karås 1979). Experiment 11 showed that roach had difficulties catching copepods which often escaped several attacks. In experiments where both cladocerans and copepods were present, roach began by attacking copepods, but after a few unsuccessful attempts they stopped attacking this kind of prey and concentrated their foraging efforts on cladocerans.

In my experiments, perch preferred daphnids when these were the same size or bigger than copepods. This contradicts results from laboratory experiments on prey selection published by Furnass (1979). When perch were offered equal numbers of Eudiaptomus gracilis and Daphnia hyalina, daphnids, which were bigger, were attacked first. After a few attacks, perch specialized in consuming copepods despite the greater number of attacks needed to strike successfully. The perch were only 3.75 cm long, so the smaller species, Eudiaptomus, was probably easier to handle than D. hyalina, because of gape limitations.

Fish size greatly influences prey selection, so different food items are preferred by larger perch and roach. Small samples, like cyclopoid nauplii and rotifers, was too small for the size of the fish used in these experiments. Cyclopoid nauplii, rotifers, ciliates and algae were consumed by perch smaller than 13 mm in Lake Windermere (Guma 1978). Cladocerans and copepods were more important food items for larger perch. Rotifers were the main food source of roach smaller than 11 mm, in Lake Sövdesjön (Johansson and Johansson 1974), but few rotifers were consumed by 23-65 mm



long roach which preferred cladocerans. The lower size limit of the prey samples in my laboratory experiments was not influenced by size when roach ranged from 60-160 mm, but was strongly influenced by perch in the same size range. This is confirmed in field studies which indicate that although even big roach consume small prey, the minimum prey size increases as the perch get bigger. This could be due to changes in the ability of perch to discover prey, to neglect of prey under a certain size or to a combination of these factors.

The anatomy of the intestine shows morphological adaptations to different feeding strategies and different rates of consumption. Perch has a relatively big stomach, whereas roach lacks a true stomach. Perch can therefore hunt for a short period and store food, but roach cannot take care of such large prey and large amounts of food in the same short period. The two species are also physiologically adapted to different rates of consumption. In laboratory experiments perch were able to consume and digest more food per day than roach (Lessmark 1983e). Characteristics of the feeding strategies are summarized in table 9.

#### 4.2. The effects of adept zooplankton predation on interspecific competition.

In numerous shallow Scandinavian lakes, perch and roach are the dominant fish species and roach is generally the most abundant (Sumari 1971, Svärdson 1976, Lessmark 1983h). There is evidence that coexisting perch and roach utilize the same kind of limited food resources and are food competitors. Where lakes contain roach, the mean biomass of perch is less than in lakes without roach (Sumari 1971, Svärdson 1976, Lessmark 1983h). On the other hand, a decline in the roach populations caused an increase in the perch populations (Lessmark 1976, Burrough et al. 1979). This proves that the presence of roach depresses perch populations.

Why is roach dominant? In many lakes different sized roach, consume the same kind of small prey, e.g. cladocerans, throughout life (Kempe 1962, Lessmark 1983h), whereas bigger perch shift to bigger prey. Since roach is more adept at foraging small prey, more of the total zooplankton biomass is available to roach than to perch. According to Svärdson (1976) and Nilsson (1978), the dominance of some fish seems to be correlated with their capacity to catch smaller zooplankton. Svärdson (op. cit.) also suggested that this may

be one of the many factors contributing to the dominance of roach over perch.

The structure of different ecosystems support the hypothesis that the fish best adapted to catching small prey dominate. Take, for example, the relations between whitefish, arctic charr and brown trout presented in the introduction. Among sunfish, bluegill (Lepomis macrochirus) handle small prey most efficiently and thus availability to open water zooplankton appears to be partly responsible for the success and dominance of this species (Werner and Hall 1979). When perch and roach were living sympatrically in Finnish lakes, the biomass of roach, perch and northern pike (Esox lucius) averaged respectively 42, 6.5 and 2.7 kg per hectare (Sumari 1971). In Lake Sövdeborgssjön, Sweden, the respective average was: 300, 40 and 40 kg per hectare (S. Hamrin Inst. of Limnology, Lund, pers. comm.). Of the three species, northern pike takes the biggest prey while roach is best adapted to small prey.

How do perch and roach compete for zooplankton? Growth rates reflect that food is limited and overlap in the utilization of food resources like zooplankton and macrobenthos is common (Lessmark 1983h). Specialization decreases competition (Nilsson and Pejler 1973, Werner and Hall 1977) and is therefore an indicator of hard competition even when there are few signs that the two species consume the same kind of food. As the young of both species mainly consume zooplankton, there seems to be severe competition for food. Specialization in the utilization of zooplankton communities by the young individuals is evident; perch select copepods and roach cladocerans. Even big perch consume zooplankton in lakes where roach is absent or rare and big zooplankton is present. In lakes where perch is the only fish species zooplankton is a more important food source (Nyberg 1979) than in lakes where they live together with roach. In a pond with sparse fish populations, the big cladocera, Daphnia magna, which was abundant, was the main food item for perch, even those perch bigger than 20 cm (Lessmark 1983h). These fish were fast-growing. In Lake Windermere, roach is rare and even big perch consume zooplankton (Allen 1935). In two Michigan lakes, Daphnia was the only zooplankton consumed by yellow perch (Perca flavescens) although there were many other genera of zooplankton (Galbraith 1967). Yellow perch in the range 7.1-24.9 cm, were very size selective and usually consumed only Daphnia over 1.3 mm long.

The size and species composition of zooplankton is conditioned by the species composition and abundance of fish. Result from this

study indicate that if roach were to disappear or its numbers be reduced in lakes dominated by perch and roach, bigger zooplankton would be more numerous and these could be utilized by big perch. Andersson et al. (Institute of Limnology, Lund, unpublished) stocked water-safe enclosures in the pelagical zone of Lake Trummen with different species of fish in the same abundance. There were no fish in one enclosure. These microcosms were in contact with the sediment and had a bottom area of 7 m<sup>2</sup>. In August, ten weeks after the start of the experiments, the big cladoceran, Daphnia longispina, was dominant in the enclosure that had no fish. A smaller cladocera, Bosmina coregoni, was dominant in the enclosure with perch, and an even smaller cladocera, Bosmina longirostris, was dominant in the enclosure with roach. This was due to the fact that roach consumed smaller zooplankton than perch. In the enclosure perch consumed the biggest cladocerans but outside the enclosure in the lake, where roach were abundant, smaller zooplankton dominated and perch consumed mainly dipterans and fish.

In this way, roach reduces the size of the dominant zooplankton by predation until they are so small that they can only be utilized by the smallest perch. This kind of indirect, diffuse competition is not reflected in the feeding overlap and cannot be monitored directly. However, this diffuse competition seems to be one of the main reasons why roach depress the perch and is the most abundant fish in many lakes.

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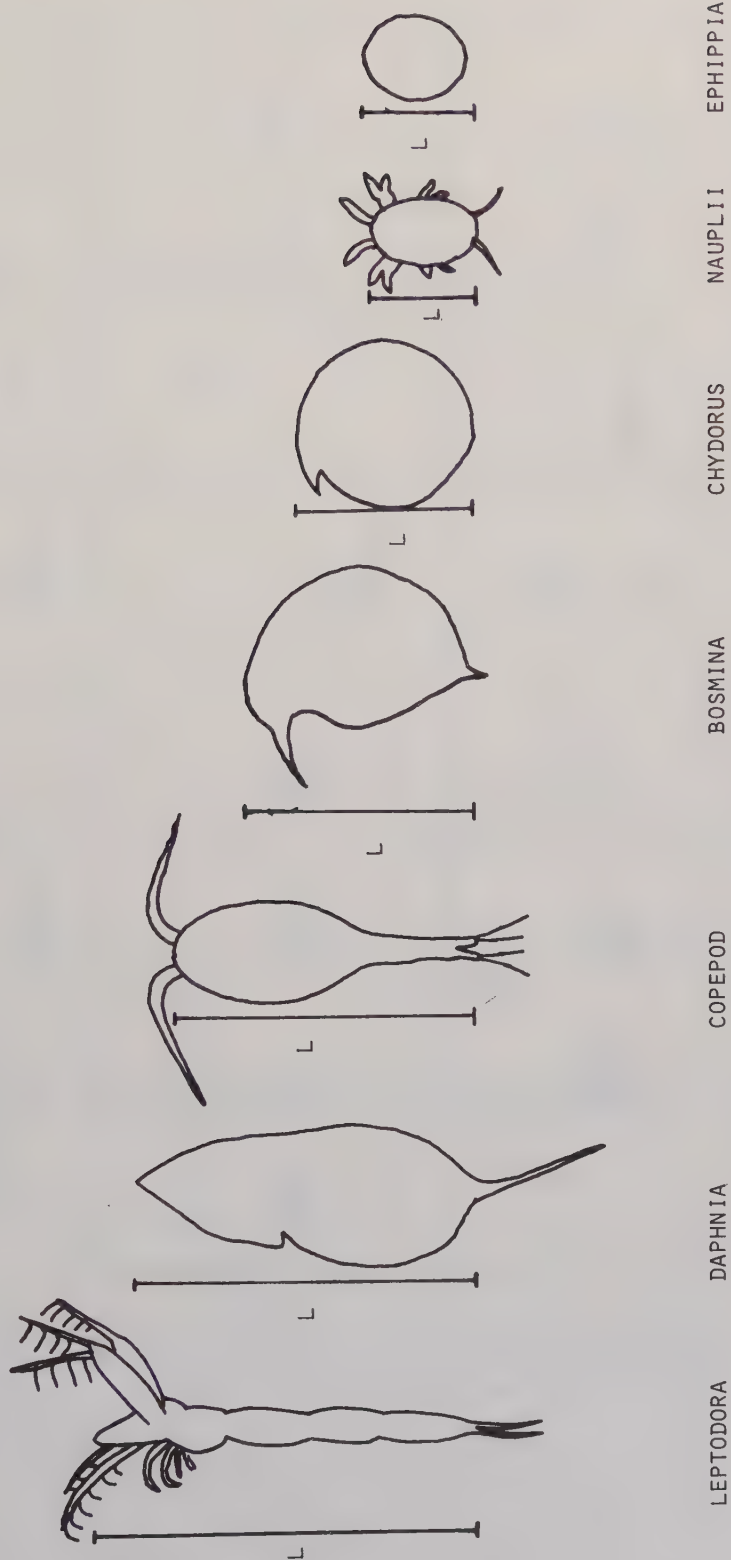
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Figure 1. Crustacean food items used in the experiments.

L denotes length of items.



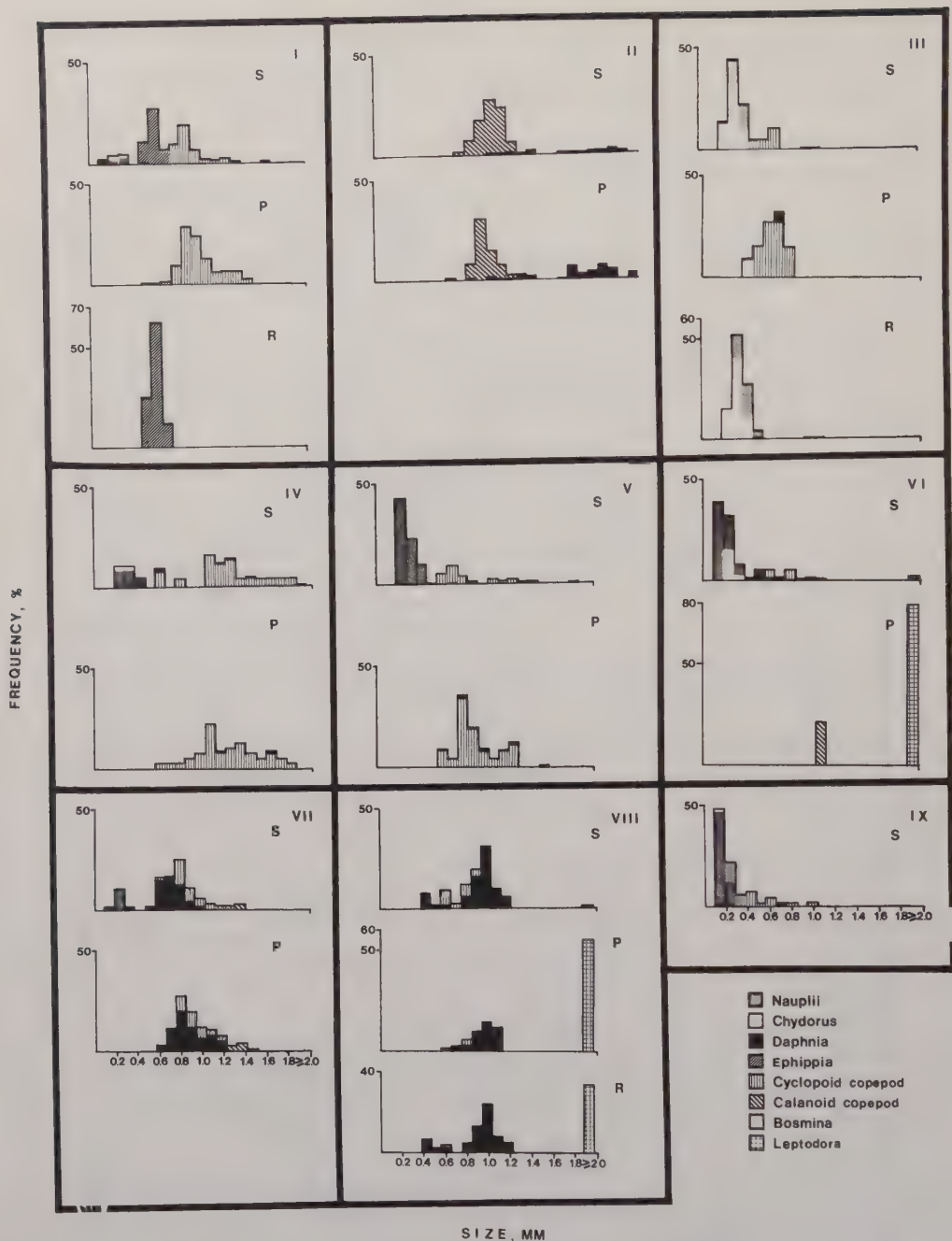


Figure 2. Size and species composition of the zooplankton used as prey samples and found in fish stomachs, in experiments 1-9, indicated by Roman numerals. S = prey samples offered to the fish  
P = prey samples consumed by perch  
R = prey samples consumed by roach

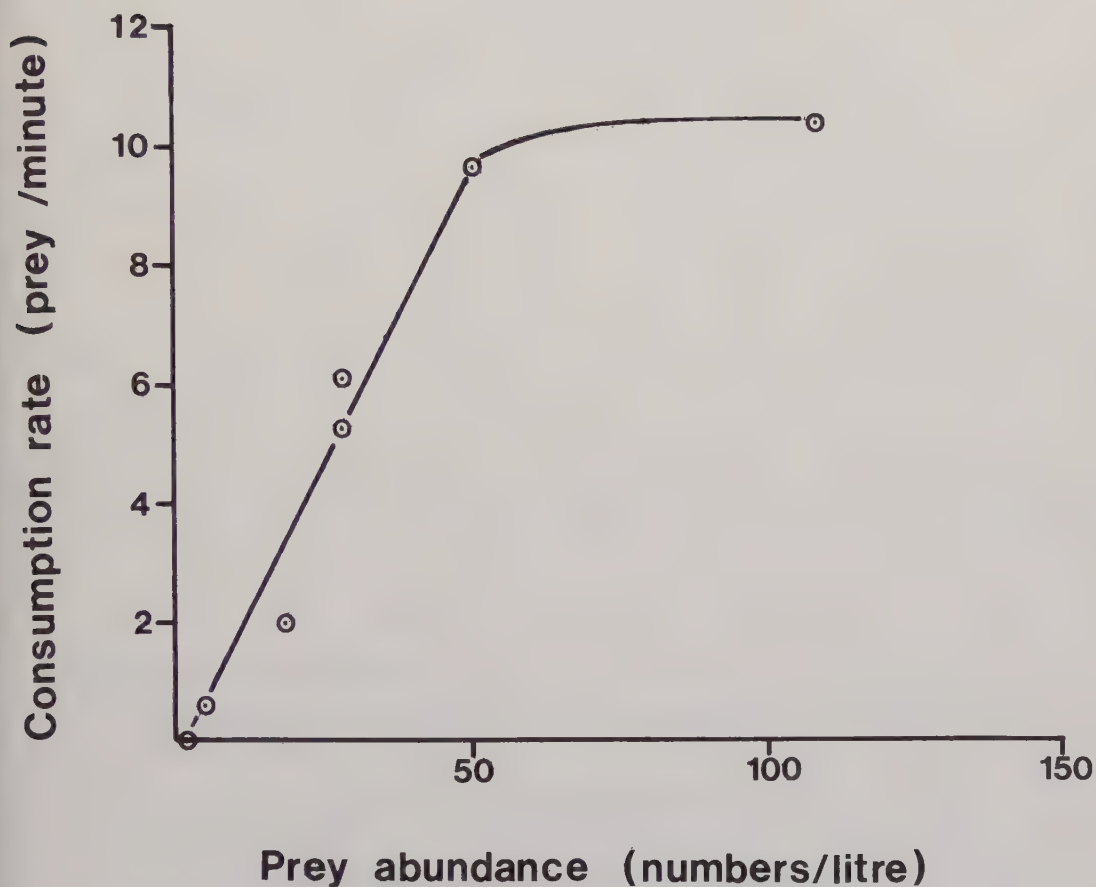


Figure 3. Rate of consumption for perch, relative to prey abundance. Prey items not consumed (copepod nauplii, ephippia, Chydorus and Bosmina) are not included in prey abundance. The line was fitted by eye.

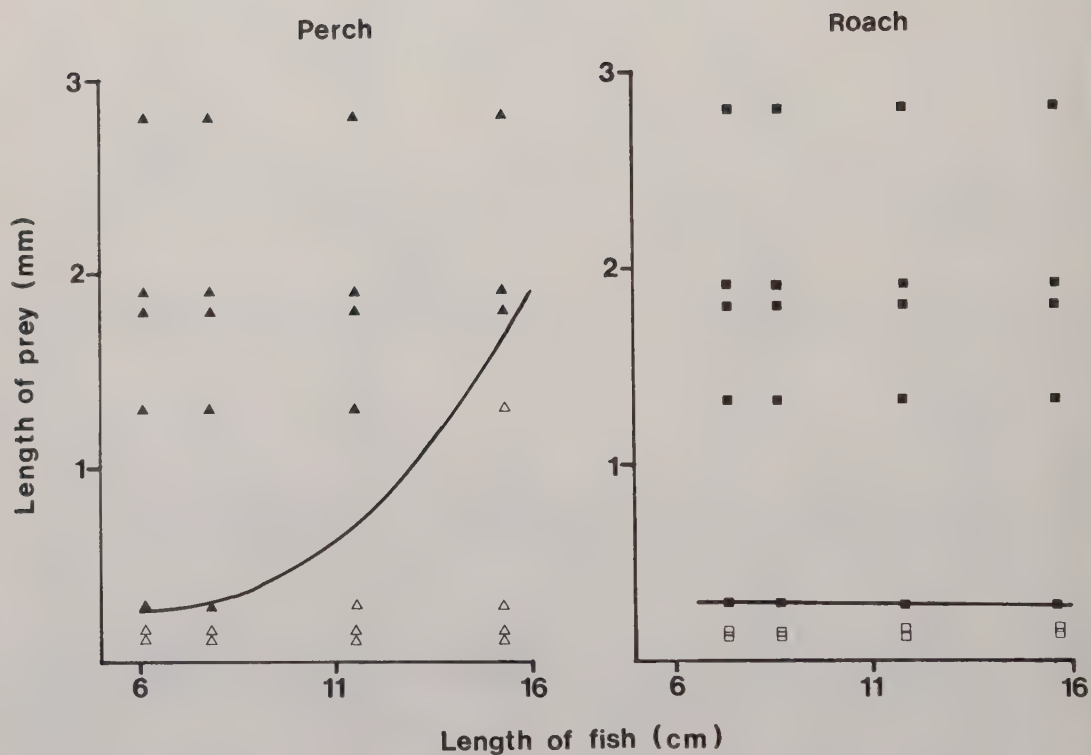


Figure 4. Correlation between length of fish and length of smallest prey consumed. Filled signs indicate that the prey was consumed and unfilled that the prey sample was not consumed. Lines were fitted by eye.



Table 1. Electivity index (E) of perch for different zooplankton in experiments 1-8.

| Zooplankton        | Experiment |       |       |       |       |       |       |       |
|--------------------|------------|-------|-------|-------|-------|-------|-------|-------|
|                    | 1          | 2     | 3     | 4     | 5     | 6     | 7     | 8     |
| Leptodora kindtii  | -          | -     | -     | -     | -     | + .97 | -     | + .95 |
| Talanoïd copepods  | -          | - .13 | -     | -     | -     | + .93 | + .31 | -     |
| Cyclopoid copepods | + .38      | -     | + .68 | + .15 | + .59 | -1    | - .07 | - .67 |
| Daphnia            | - .33      | + .30 | + .55 | - .03 | + .66 | -1    | + .11 | - .38 |
| Bosmina            | -          | -     | - .89 | -     | -     | -     | -     | - .61 |
| Chydoridae         | -1         | -     | - .77 | -1    | -     | -1    | -     | -     |
| Copepod nauplii    | -1         | -     | -1    | -1    | -1    | -1    | -1    | -     |
| Ephippies          | -1         | -     | -     | -     | -     | -     | -     | -     |

Table 2. Electivity index (E) of roach for different zooplankton in experiment 1,3 and 8.

| Zooplankton        | Experiment |       |       |
|--------------------|------------|-------|-------|
|                    | 1          | 3     | 8     |
| Leptodora kindtii  | -          | -     | + .92 |
| Cyclopoid copepods | - .89      | -1    | -1    |
| Daphnia            | - .67      | + .23 | - .10 |
| Bosmina            | -          | + .12 | - .16 |
| Chydoridae         | -1         | + .10 | -     |
| Ephippies          | + .40      | -     | -     |
| Copepod nauplii    | -1         | -1    | -     |

Table 3. Mean size of zooplankton prey samples and the zooplankton in perch stomachs in experiments 1-9.

| Experiment | Mean size of zooplankton (mm) |                   | $\chi^2$ -test |
|------------|-------------------------------|-------------------|----------------|
|            | Prey sample offered           | In perch stomachs |                |
| 1          | 0.71                          | 1.02              | $p < 0.001$    |
| 2          | 1.20                          | 1.40              | "              |
| 3          | 0.40                          | 0.63              | "              |
| 4          | 0.98                          | 1.24              | "              |
| 5          | 0.43                          | 0.91              | "              |
| 6          | 0.33                          | > 2               | "              |
| 7          | 0.72                          | 0.92              | "              |
| 8          | 0.96                          | > 2               | "              |
| 9          | 0.24                          | -                 | -              |

Table 4. Mean size of Daphnia prey samples and the Daphnia in perch stomachs.

| Experiment | Mean size of <u>Daphnia</u> (mm) |                   | Mann-Whitney U-test |
|------------|----------------------------------|-------------------|---------------------|
|            | Prey sample offered              | In perch stomachs |                     |
| 2          | 1.68                             | 1.84              | $p > 0.05$          |
| 7          | 0.72                             | 0.87              | $p < 0.001$         |
| 8          | 0.90                             | 0.96              | $p > 0.05$          |

Table 5. Mean size of copepod prey samples and the copepods in perch stomachs.

| Experiment      | Mean size of copepods (mm) |                      | Mann-Whitney<br>U-test |
|-----------------|----------------------------|----------------------|------------------------|
|                 | Prey sample<br>offered     | In perch<br>stomachs |                        |
| 1               | 0.92                       | 1.01                 | p < 0.001              |
| 2               | 1.07                       | 1.01                 | p < 0.01               |
| 3               | 0.66                       | 0.65                 | p > 0.05               |
| 4               | 1.22                       | 1.24                 | p > 0.05               |
| 5               | 0.83                       | 0.91                 | p < 0.05               |
| 7               | 0.90                       | 0.93                 | p > 0.05               |
| 7 <sup>\$</sup> | 1.17                       | 1.29                 | p > 0.05               |

<sup>\$</sup> calanoid copepods, all other cyclopoid.

Table 6. Number of prey of different sizes consumed by perch and by roach, when the fish were randomly offered prey from the two different size classes.

| Prey size      | Number of prey samples<br>consumed |       |
|----------------|------------------------------------|-------|
|                | Perch                              | Roach |
| Big D. magna   |                                    |       |
| 2.52-3.35 mm   | 39                                 | 11    |
| Small D. magna |                                    |       |
| 1.04-1.39 mm   | 11                                 | 39    |

Table 7. Number of attacks per prey on different prey samples before they were consumed by perch and by roach.

| Prey type | Number of attacks / prey sample consumed ( $\pm$ S.D.) |                |
|-----------|--------------------------------------------------------|----------------|
|           | Perch                                                  | Roach          |
| Copepod   | 1.2 $\pm$ 0.09                                         | 3.7 $\pm$ 1.01 |
| Daphnia   | 1.0 $\pm$ 0.00                                         | 1.0 $\pm$ 0.00 |

Table 8. Respective rates of consumption for perch and roach for different kinds of prey.

| Prey type             | Consumption rate (numbers/20 minutes) |       |
|-----------------------|---------------------------------------|-------|
|                       | Perch                                 | Roach |
| Chaoborus             | 4.6                                   | 2.0   |
| Leptodora and Daphnia | 40                                    | 15    |

Table 9. Feeding characteristics for perch and for roach.

| Factors affecting feeding                                | Roach                  | Perch                     |
|----------------------------------------------------------|------------------------|---------------------------|
| Minimum size of prey (mm) <sup>\$</sup>                  | 0.3                    | 0.5                       |
| Locomotion of prey                                       | immobile - slow-moving | slow-moving - fast-moving |
| Feeding strategy                                         | cropping               | hunting                   |
| Consumption rate                                         | low                    | high                      |
| Correlation: minimum prey size/fish size <sup>\$\$</sup> | no correlation         | strong correlation        |

\$ for 7-8 cm long fish when different sized prey was available

\$\$ for fish 6-16 cm long





INFLUENCE OF ABIOTIC AND BIOTIC FACTORS ON THE  
STRUCTURE OF PERCH AND ROACH POPULATIONS IN  
THIRTEEN SWEDISH LAKES, WITH SPECIAL REFERENCE  
TO INTERSPECIFIC COMPETITION

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## SUMMARY

The structure of the perch and roach populations in 13 Swedish lakes with widely differing limological characteristics, was not directly related to any of the abiotic factors: lake area, depth, transparency or phosphorus concentration.

Biotic factors were far more important. Blue-green algae was important as food for roach and high biomass resulted in numerous populations of slow-growing fish with low mean-length and size-class diversity. Roach preferred animal food and grew faster on an animal diet than on a vegetable diet. Size of zooplankton was important and the presence of big cladocerans resulted in fast growth of perch and roach. The number of crustaceans, however, was insignificant for individual growth and for the population structure of the populations.

Perch grew fastest during the first two years of life where there was a high abundance of big cladocerans. Although there was no competition for food and big cladocerans were abundant, older perch grew faster on a fish-diet in another lake where there was a high abundance of small roach suitable as food.

Intraspecific competition between perch for benthos was most negative for the biggest of the benthos-feeding fish, and perch reached a bottle neck at the change-over from the benthos-feeding stage to piscivory.

Vegetable food became more important in the diet of roach when intraspecific competition for animal food was strong. Intraspecific competition between roach was most severe to the biggest fish. Their diet was more vegetarian than that of smaller fish and growth was more retarded.

Interspecific competition between perch and roach for benthos and zooplankton, had a negative affect on the growth and abundance of small perch. In the shallowest lakes, perch and roach were the most dominant fish species and roach was more numerous than perch. This could be correlated to the total food resources, which were bigger for roach than for perch since roach used smaller zooplankton species more adeptly than perch and besides this, also utilized plants and detritus as food. The roach populations were mainly regulated by intraspecific competition. For perch, interspecific competition was more important.

In the deepest lakes, planktivorous small bream, white bream and vendace were abundant and were important food competitors, especial-

ly for roach.

Thus, roach strongly influenced the population structures of perch. Perch, however, did not have a significant influence on the roach populations, which were regulated by intraspecific food competition and in deeper lakes also by interspecific food competition with bream, white bream and vendace.

The effect of roach on the plankton community, changing composition of zooplankton towards smaller sizes and increasing biomass of blue-green algae favours roach and disfavours perch. In my opinion, these diffuse competition mechanisms are the most important factors making roach more numerous than perch, in eutrophic lakes.

## INTRODUCTION

Around 1970 I noticed that the perch (Perca fluviatilis) populations in two lakes where perch and roach (Rutilus rutilus) dominated, increased rapidly as the roach populations declined (Lessmark 1976). Strong competition was evident as limited food resources were shared by these species. In Finnish lakes dominated by perch and roach, competition between the two species was also evident (Sumari 1971). Roach was generally more abundant than perch, but in lakes where roach was absent, perch had a higher biomass than in lakes where both species were present. Further evidens for interspecific interactions between perch and roach was presented by Svärdson (1976), Burrough et al. (1979), Stenson (1979) and Persson (1983c).

Perch and roach are common fish species in Swedish lakes in the south to far up in the north with the exception of high altitude mountain lakes (Ekman 1922). Perch and roach are best adapted to high temperatures (Lessmark 1983e). Growth is fastest in the summer. They are visual feeders, active mainly in the daytime (Lessmark 1983g).

The aim of this study is to estimate the importance of abiotic and biotic environmental factors for the population structures of perch and roach in lakes in southern Sweden. The interactions between perch and roach have been stressed.

## THE LAKES

The study comprises 13 lakes situated in southern Sweden (Fig. 1), in which perch and roach, or either of them, are important species. The lakes ranged from oligotrophic to hypertrophic. Extensive limnological studies have been performed in most of the lakes. Data used to characterize the lakes (Table 1) are from July or August of the same years the fish fauna was studied. The values for phosphorus concentration and biomass of blue-green algae are from the upper 2 m water-layer. Using a relative method, zooplankton was classified according to the size of daphnids, in the following way: class 1: the small-sized Daphnia cucullata or D. cristata occurred, class 2: the larger species D. longispina or D. galeata were present, and class 3: the even larger species D. magna or D. pulex occurred. When different-sized Daphnia were found in the same sample, the largest was used for classification.

The four deepest lakes Lakes Fegen, Kalvsjön, Flaten and Magelungen were thermally stratified in summer, with a large, well-developed hypolimnion. There was oxygen deficiency in the deeper parts of the hypertrophic Lake Magelungen during long periods of the year and in small areas of Lakes Trekanten, Laduviken, Långsjön and Pond Habo in the summer. Lakes Björnsjön and Låen were slightly acidified.

## METHODS

### Test fishing

In 12 of the 13 lakes, fish were caught with gill-nets of several mesh-sizes, to catch fish of a broad size range. In most lakes, I used 1.5 m deep gill-nets of twined nylon with 8 different 7 m-long net sections. Knot to knot mesh-sizes were: 9.5, 14.5, 18, 24, 29.5, 33, 38 and 40 mm. In one lake, Lake Trummen these gill-nets were supplemented with two 7 m-long net sections of mesh-sizes 13 and 16 mm. In Lake Sövdeborgssjön in 1980, another kind of gill-net was used. These were 3 m deep and 30 m long, composed of 8 different nets of mesh-sizes 7.6-50 mm. The gill nets were set on the bottom of the lakes at several depths in July, August or September. They were set in the morning and examined after 24 hours.

Roach and perch prefer warm epilimnion water to the cooler meta- and hypolimnion water and were only occasionally found below the epilimnion. Only catches above the thermocline and from depths with higher oxygen concentrations than  $2 \text{ mg l}^{-1}$  were used in the estima-



tion of fish-population characteristics.

In Pond Habo, the fish were taken with a fine-meshed fyke net in different seasons.

Gill-nets catch fish selectively as regards size and species (Hamrin 1979). Since the fish are caught passively, the catch depends on the activity of the fish. Morphology and behavioural patterns thus influence the catch in gill-nets. Also, when gill-nets of several mesh-size are used, the catch is not representative for the entire fish-populations. However, the information can be used for relative descriptions and comparisons of the fish populations in different lakes.

In Lake Trummen, the gill-nets used were larger in area than those used in the other lakes. The difference was judged to be small and not significant considering the purpose of this study. In Lake Sövedborgssjön the gill-nets were different and consequently the catches were not comparable with those from the other gill-nets. These were therefore excluded from the regression analyses. Due to, the fishing method used in Pond Habo, growth could only be estimated.

#### Population characteristics

Abundance of fish was estimated relatively as mean number of fish caught per gill-net and day. Numerical proportion of roach to perch was estimated as percentage roach of the total number of roach plus perch.

Size-class distribution of perch and roach was estimated from measurements of the total length of fish caught in gill-nets. Size-class diversity was measured by the Shannon-Wiener function:

$$H = -\sum_{i=1}^s (p_i) (\log_2 p_i)$$

where  $H$  = index of size-class diversity,  $s$  = number of size-classes and  $p_i$  = proportion of total sample belonging to  $i$ :th size-class (Krebs 1972).

Growth of the fish was estimated by back-calculations of length at different ages, on the opercula of perch according to Le Cren (1947) and on the scales of roach according to Kempe (1962). For growth analysis, fish from the catches were selected so that the different size-classes were equally represented in the samples. 16 to 60 fish were analysed from each lake and species. Several year classes were included in the samples and mean lengths at specific ages were calculated. This gave mean values of growth during several

years and reduces the effect of atypical values for certain years. It was frequently difficult to estimate the position of the first annual mark on the opercula of perch and the lengths of one-year old perch were excluded from the presentation.

Length values were transformed to weight values using equations for the length-weight relationship. For perch, the equation was calculated from length-weight data of 7-30 cm-long fish from Lake Laduviken. For roach the equation was calculated from data for generally 5 fish from each cm-class in the range 7-30 cm. These fish were taken from several of the lakes. Separate length-weight equations for the different lakes would have been more correct if the fish had been taken at the same time of year. As the length-weight relationship differs during the year, a general, common equation was used for all lakes to moderate the effect of different sampling periods and to give more comparable values. Another reason for using general length-weight equations for all populations was that in some lakes it was impossible to get fish from all size-classes equally represented in the samples.

Food availability affects growth. A measure of the magnitude of food competition can be obtained by comparing growth in environments with and without food-competition. Thus, annual growth can be used to monitor the harmful effects of competition during different life-stages. If growth of fish in different lakes is to be used as a measure of food-availability, the temperature must be similar as this strongly influences growth. The mean temperature during summer at the studied lakes varied so little that this factor can be ignored.

Perch grew faster than roach and attained higher weights at specific ages in most of the lakes in this investigation. However, to interpret this as proof that perch is always relatively more favoured than roach, would be incorrect. It is not possible to evaluate which species suffered most from food-competition at different stages of life by making direct growth comparisons, since the maximum possible growth-rate is higher for perch than for roach (Lessmark 1983e). The fish populations in Pond Habo were sparse and animal food was abundant. Perch and roach grew fast and growth was probably not reduced by competition for food. It is therefore possible to use Pond Habo as a reference for maximum potential growth when there is no food-competition.

In Lakes Läen and Björnsjön, reproduction of roach had ceased due to acidification. The remaining roach were too few to make a characterization of the population meaningful.

## Food

I examined the gut content of 5 fish per 5 cm size-class and species, when possible, from lakes Trekanten, Laduviken and Trummen. The food was estimated semi-quantitatively as dominant or occurring. In Lakes Björnsjön and Låen, energy values for the gut content of perch were estimated (Lessmark 1976).

It was difficult to identify and quantify the food of roach since the gut commonly contained a mixture of animal- and plant-matter and detritus which had been minced by the pharyngeal mill. The purely animal diet of perch was easy to identify and quantify.

According to the analyses, much of the gut content of roach was classified as detritus. However, in aquarium experiments with roach, I found that blue-green algae quickly changed colour and structure in the gut and looked like algal detritus (Lessmark 1983f). Since blue-green algae were very abundant in many lakes, much of the food that was classified as detritus, should probably more correctly have been classified as blue-green algae.

The food data for fish in Pond Habo was supplied by Dr Gunnar Andersson, Institute of Limnology, Lund.

Insect larvae and other invertebrates, apart from zooplankton, have most often been treated as a group and have been called benthos.

## Regression analyses

I used linear regression to analyse whether there was any relationships between the population characteristics of perch and roach and the abiotic and biotic conditions in the lakes.

First, I analysed the relationships between fish population characteristics and the abiotic factors: maximum, mean and epilimnion depth, area, transparency and total phosphorus concentration in the water.

Then, I analysed the relationships between fish population characteristics and the biotic factors: size of zooplankton, abundance of crustaceans and biomass of blue-green algae in the water.

Finally, I analysed the relationships between the different fish population characteristics. The F-test was used to test significance of the regressions.

## RESULTS

### Structure of the fish populations

Perch and roach were dominating in Lakes Trekanten, Laduviken, Långsjön, Trummen and Sövdeborgssjön, abundant in Lakes Fegen, Kalvsjön, Flaten and Magelungen and rare in Pond Habo (Fig. 2, Table 2). Up to 1980, bream was more abundant in Lake Trummen, because of immigration from a lake located downstream. However, prevention of immigration and extensive fishing of bream in the years 1976-80 heavily reduced the bream population.

In the hypolimnion of Lakes Fegen and Kalvsjön the planktivorous vendace was abundant and the mean catch per gill-net and day was 39 for Lake Fegen and 20 fish for Lake Kalvsjön.

Perch was the most abundant species in Lakes Björnsjön and Län where slight acidification prevented roach from reproducing.

Roach was dominating and perch was absent in Lake Lillesjön.

Rapid growth and high abundance of large-sized cladoceran species indicated fish populations in Pond Habo were sparse.

A total of 19 fish species occurred in the lakes (Table 2).

Size-class diversity and mean length were highest for perch in Lake Trekanten and lowest for perch in Lake Sövdeborgssjön, in 1980 (Fig. 3, Table 3). Size-class diversity and mean length were highest for roach in Lake Flaten and lowest in Lake Trekanten (Fig. 3, Table 3).

### Food

The diet of perch consisted of zooplankton, benthos and fish (Table 4). Feeding was influenced by perch-size and the quality and quantity of available food resources. In Lakes Trummen, Trekanten, Laduviken (in 1980), Län and Björnsjön (Fig. 4) the size and kind of prey changed according to perch-size. Zooplankton were small and were only consumed by the smallest perch in Lakes Trekanten and Laduviken. The larger zooplankton in Pond Habo were consumed by perch of all sizes. In most of the lakes only the largest perch consumed fish, but in Lake Laduviken in 1981 even the smallest perch consumed fish. Huge schools of small, young of the year roach, too small to be caught in the gill-nets, were observed in Lake Laduviken at the same time and perch of all sizes exploited this food source.

In Lakes Län and Björnsjön the diet of perch smaller than 20 cm consisted mainly of benthos, and that of larger perch consisted mainly of fish (Fig. 4). Among the benthos-feeding perch, the energy va-



lue of the gut content per weight of fish was highest for the smallest fish. When perch became large enough to feed on fish, their food-intake increased. Food-shortage affected most severe 150-199 mm long perch which were too small to consume fish and too large to use benthos efficiently.

Perch, in all of the lakes, fed opportunistically. Food items were more related to size than to taxonomical group.

Roach was omnivorous, with a diet of detritus and plant material, zooplankton and benthos. Vegetable food and detritus was more dominant in the guts of large fish than of small.

Both perch and roach utilized zooplankton and benthos. Vegetable food and detritus was utilized only by roach and fish were consumed only by perch.

### Growth

Slower growth of perch (Fig.5) and roach (Fig. 6) compared to Pond Habo, indicated that there was strong competition for food in most of the lakes. Perch grew faster than roach and attained higher weights at specific ages in most of the lakes (Fig. 7). Two year old perch from Pond Habo weighed approx. 10 times more than those from Lakes Trummen, Långsjön, Magelungen and Sövdeborgssjön (Fig. 5). There was also about a 10 fold difference in the weight of 6-yr old perch. Like in most of the lakes, perch grew slowly in Lake Trekanten during the first two years of life, but there-after growth was faster than in most of the other lakes. Roach grew fastest in Lake Lillesjön and Pond Habo and slowest in Lakes Trekanten and Sövdeborgssjön (in 1980) (Fig. 7). The difference in weight between the population that grew the fastest and the slowest growing population was more than tenfold for fish older than 2 years. If growth was slow during the first 2 years it generally continued to be slow. At all ages, the growth of roach was more uniform than that of perch, whose growth-rate increased more abruptly than that of roach in some lakes in connection with a change in diet.

### Fish population characteristics in relation to abiotic factors

Weight of 4-year old ( $r^2 = 0.59$ .  $p < 0.01$ ) and 2-year old perch were positively related to concentration of phosphorus in the water (Table 5). If Pond Habo is excluded from the regression there is no relationship between weight of 2-year olds and phosphorus concentration ( $r^2 = 0.00$ ). There was no relationship between abundance, mean



length or diversity of perch and any abiotic factor.

The weights of 2- and 4-year old roach were not related to any abiotic factors, but the weights of 6-years old ( $r^2 = 0.70$ ,  $p < 0.1$ ) and 8-year old were negatively related to phosphorus concentration. Abundance of roach was negatively related to transparency ( $r^2 = 0.56$ ,  $p < 0.01$ , Fig. 8). Mean length was positively related to transparency ( $r^2 = 0.76$ ,  $p < 0.001$ , Fig. 9) and negatively related to phosphorus concentration ( $r^2 = 0.65$ ,  $p < 0.01$ , Fig. 10). Mean length was also positively related to depth. However, the deepest lakes were also the most oligotrophic and had the highest transparency, and depth was not the most important factor. Size-class diversity was negatively related to phosphorus concentration ( $r^2 = 0.43$ ,  $p < 0.05$ , Fig. 11) and positively related to transparency ( $r^2 = 0.34$ ,  $p < 0.1$ , Fig. 12).

The numerical proportions between roach and perch were negatively related to transparency ( $r^2 = 0.68$ ,  $p < 0.01$ , Fig. 13), and maximum depth ( $r^2 = 0.56$ ,  $p < 0.05$ , Fig. 14), and positively related to phosphorus concentration ( $r^2 = 0.52$ ,  $p < 0.05$ , Fig. 15).

#### Fish population characteristics in relation to biotic factors

Except for a positive relationship between weight of 2-year olds and size of zooplankton ( $r^2 = 0.77$ ,  $p < 0.01$ ), there were no significant relationships between the population characteristics of perch and biotic factors.

There were negative relationships between the biomass of blue-green algae and the diversity ( $r^2 = 0.75$ ,  $p < 0.01$ , Fig. 16) and mean length ( $r^2 = 0.68$ ,  $p < 0.01$ , Fig. 17) of roach. There was no significant relationship between the weight of 2- and 4-year old roach and blue-green algae biomass, but there was negative relationships between the weights for 6-year olds ( $r^2 = 0.89$ ,  $p < 0.05$ ) and 8 year olds ( $r^2 = 0.88$ ,  $p < 0.1$ ) and biomass of blue-green algae. There was no relationship between growth and the abundance of zooplankton, but growth was positively related to the size of zooplankton for 2-year olds ( $p < 0.05$ ) and 4-year olds ( $p < 0.1$ ). The regressions were strongly dependent on values from Pond Habo, as the regressions were not significant when these were excluded. However, Pond Habo was the only water body with zooplankton of size-class 3. An increase in the biomass of blue-green algae, caused an increase in the abundance of roach, compared to perch ( $r^2 = 0.56$ ,  $p < 0.05$ , Fig. 18).

## Fish population characteristics in relation to each other

There was no relationship between the weight of 2-years old perch and the abundance of perch ( $r^2 = 0.00$ ) but the relationship was negative between 2-year old perch and the abundance of roach ( $r^2 = 0.45$ ,  $p < 0.1$ , fig. 19) as well as the abundance of all fish ( $r^2 = 0.59$ ,  $p < 0.05$ , Fig. 20). Mean length of perch was negatively related to the abundance of roach ( $r^2 = 0.41$ ,  $p < 0.1$ , Fig. 21) and the abundance of all fish ( $r^2 = 0.48$ ,  $p < 0.05$ , Fig. 22).

The weights of roach, at 6 years old ( $r^2 = 0.75$ ,  $p < 0.1$ , Fig. 23) and 8 years old ( $r^2 = 0.96$ ,  $p < 0.05$ , Fig. 24), mean length of roach ( $r^2 = 0.55$ ,  $p < 0.05$ ) and size-class diversity of roach ( $r^2 = 0.43$ ,  $p < 0.05$ ) were negatively related to abundance of roach. Mean length of roach was positively related to the weight of 6-year olds ( $r^2 = 0.73$ ,  $p < 0.1$ , Fig. 25) and 8-year olds ( $r^2 = 0.88$ ,  $p < 0.1$ , Fig. 26). Size-class diversity was positively related to weight at 6 years old ( $r^2 = 0.82$ ,  $p < 0.05$ , Fig. 27) and at 8 years old ( $r^2 = 0.93$ ,  $p < 0.05$ ). There was no significant relationship between the growth of roach and the abundance of perch.

## DISCUSSION

### Abiotic factors

Relationships between the population characteristics of roach and phosphorus concentration and transparency were dependent on the fact that when the concentration of phosphorus in the lakes increased, the biomass of blue-green algae, which is a valuable food increased and transparency decreased. Regressions with abiotic factors were, in fact, less significant than those with blue-green algae. Abiotic factors are important to perch and roach but biotic factors had a stronger affect. Sumari (1971) also found that biotic factors such as predation, food competition and available food were far more important for the population structures of perch than abiotic factors were. No abiotic factors were directly related to the population structures of perch and roach.

### Blue-green algae as food for roach

In laboratory experiments, roach fed on blue-green algae grew considerably. Green algae did not have the same effect (Lessmark 1983f). However, compared to animal food, blue-green algae was a

second class food and growth was slower than on an animal diet.

Blue-green algae were abundant in Pond Habo but unimportant as food for roach because big cladocerans were abundant. Roach preferred cladocerans. A diet of these resulted in fast growth of roach.

In Lake Sövdeborgssjön, the diet of roach was dominated in 1975 by chironomids (Johansson and Lundahl 1976) and in 1980, by detritus and blue-green algae (Persson 1983b). Roach grew faster in 1975 than in 1980. In the River Stour, England, roach had a largely carnivorous diet and grew faster than in most European waters (Mann 1973). Although roach prefer animal food and grow faster on an animal diet, blue-green algae are a food resource of quantitative importance (Sorokin 1968, Lyagina 1972, Lessmark 1983f) which is the reason for an abundance of slow-growing roach in many eutrophic lakes. Intensive intraspecific competition for zooplankton contributes to the slow growth, low size-class diversity and mean length values for roach. Hard predation pressure by roach on zooplankton often causes small zooplankton species to dominate where there is a high biomass of blue-green algae. The relatively larger proportion of vegetable food consumed by larger fish indicates that the larger fish suffer more from a lack of animal food. Kémpe (1962) also found that the proportion of plants in the diet increased with the size of roach. Mann (1973) found roach to be mainly carnivorous, but filamentous algae were found more frequently in larger fish.

#### Importance of zooplankton

In experimental studies with fish of the same size, it was found the smallest sized zooplankton taken by perch was bigger than the smallest size taken by roach (Lessmark 1983g). In the lakes where the zooplankton species were relatively small, these were consumed only by the smallest perch, whereas also bigger roach consumed zooplankton. The larger zooplankton in Pond Habo were consumed by both perch and roach of all sizes and growth was fast. It was the size of planktonic crustaceans but not the number, which was important for the growth of perch and roach.

#### Importance of interactions between fish

Several of the population characteristics for perch were related to the structure of the roach populations. Population characteristics of roach were related to another but were not influenced by perch. This indicated that, in contrast to abiotic factors, inter-

and intraspecific interactions were important for the population structures of perch and roach. For perch, interspecific interactions were most important and intraspecific interactions were relevant mainly for roach.

In Pond Habo where fish populations were sparse and there was no food competition, both perch and roach consumed the same kind of food, i.e. big cladocerans. In the other lakes, strong food competition caused a feeding niche separation which reduced the feeding overlap. Feeding became more specialized according to what the two species were best adapted to. This meant that perch consumed big, mobile prey and that roach fed on detritus and plant material. Small perch consumed the snatchy moving copepods which were difficult for roach to catch (Lessmark 1983g). Roach fed more on cladocerans than copepods. Roach consumed smaller prey than equal-sized perch and they consumed zooplankton throughout life, whereas benthos gradually became more important for perch as the perch grew bigger.

Despite feeding separation and food-type specialization, strong inter- and intraspecific competition for zooplankton and benthos was evident.

#### Lake categories

To facilitate a comparison and evaluation of the effects of inter and intraspecific competition, the lakes were classified into groups on the basis of fish faunas.

1. Perch lakes. In Lakes Björnsjön and Län it was possible to study only intraspecific interactions between perch, because perch was the only species of importance.

Intraspecific competition was most severe among the largest benthivorous perch. Perch experienced a bottleneck situation before they became big enough to be piscivorous, which considerably improved food intake and growth. This type of bottle neck effect was more pronounced in Lake Län than in Lake Björnsjön, where cannibal perch were more numerous and thinned out small perch. The effects of intraspecific competition on the growth and population structure of perch and growth improvement by cannibalism were similar to those described by Alm (1946) and Sumari (1971).

2. Roach lake. Roach grew fastest in Lake Lillesjön. A severe fish-kill due to oxygen deficiency on winter some years before the investigation, thinned out the population. Reduced food competition explains the fast growth, which even exceeded that in Pond Habo. This may depend on differences in summer temperatures.



3. Perch-roach lakes. In Lakes Trekanten, Laduviken, Trummen, Sövdeborgssjön and Långsjön, perch and roach were the most common fish and other species were poorly represented. It was therefore possible to evaluate the importance of interactions between perch and roach in these lakes.

The large roach population in Lake Trekanten was dominated by small, slow-growing fish due to the high biomass of blue-green algae and the importance of blue-green algae as food. Slow growth of young roach and perch resulted from strong competition for zooplankton and benthos. Due to this fact, the mortality of young perch was probably high. The roach population was much bigger than the perch population and roach were probably more affected by intraspecific competition than perch. Perch were more affected by interspecific competition. The high abundance of small roach hastened piscivory among perch. Thus, roach influenced perch by food-competition, reduced growth and abundance of perch. Despite a large population of piscivorous perch, the population characteristics of roach did not seem to be significantly influenced. If perch had significantly reduced the roach population, intraspecific competition between roach would have been reduced and roach would have grown faster.

Roach grew faster and was less abundant in Lake Laduviken than in Lake Trekanten, probably due to the fact that blue-green algae biomass was less in Lake Laduviken. This reduced the influence of roach on perch and, for the first two years, perch grew faster in Lake Laduviken than in Lake Trekanten.

Oxygen deficiency caused a heavy fish-kill in Lake Sövdeborgssjön in the winter of 1969-70 (Andersson and Gelin 1970), which explains why the fish populations were so different in 1975 and in 1980. In 1975, the numbers of perch and roach were the same, but in 1980 roach were more numerous. After the fish kill, perch recovered faster than roach, probably because perch is better physiologically adapted than roach to utilizing a large supply of animal food and to grow faster than roach (Lessmark 1983e). Food abundance per fish was probably higher after the fish-kill. The size of zooplankton is largely influenced by fish-density and it is likely that bigger zooplankton species were more common just after the fish kill than when the fish populations had recovered. Roach consume smaller zooplankton than perch and also vegetable food when animal food is in short supply. These factors favour roach more than perch when the abundance of fish and competition for animal food increases.



In Lakes Trekanten and Sövdeborgssjön in 1980, the roach populations dominated by small individuals feeding on pelagical food, were similar but the perch populations were different. The perch in Lake Sövdeborgssjön were small. Only a few became big and piscivorous like those in Lake Trekanten. This was probably due to the littoral zone in L. Sövdeborgssjön, which consisted of a broad belt of water lillies and comprised 30 % of the lake area. Benthos, living in the littoral, was the prevailing food for perch in Lake Sövdeborgssjön (Persson 1983a) and slow growth indicated strong food competition. In L. Trekanten the shores were step and the macrophyte vegetation covered only 3 % of the lake area. Pelagical food resources were more important than in Lake Sövdeborgssjön, so that perch consumed more pelagical food and had to compete with roach in the open water. This disfavoured young perch and reduced the numbers of benthivorous perch in Lake Trekanten more than in Lake Sövdeborgssjön, thus reducing intraspecific competition and making it easier for perch to attain roach-eating size. In this way, the proportional size of the littoral zone to the total lake area is important for perch.

4. Perch-roach-bream/white bream-vendace lakes. In the four deepest lakes, Lakes Fegen, Kalvsjön, Flaten and Magelungen, perch and roach were less dominant than in the other lakes. Interference from the many other common species made it impossible to accurately evaluate the importance of interactions between perch and roach.

The competition between roach, bream/white bream and vendace was complex. In the shallowest lakes, roach dominated the fish fauna numerically, vendace were absent and bream/white bream few or absent. In the deeper lakes, either bream/white bream or vendace was more common species. Vendace is adapted to low temperatures and lives in summer in the cold hypolimnion water, due to this fact vendace was absent in the shallowest lakes. Bream/white bream are, however, adapted to higher temperatures and live in the epilimnion water. There was evidence of hard competition for zooplankton between vendace and small bream/white bream, which resulted in a low abundance of bream/white bream. In Lakes Flaten and Magelungen, where vendace were absent, bream/white bream were abundant and the populations were dominated by small individuals with mean-lengths of 14.4 cm respectively 15.1 cm. In Lakes Fegen and Kalvsjön, vendace were abundant and bream, few and rather big with mean lengths of 33.1 cm respectively 29.5 mm.

The presence of vertically migrating copepods in deep lakes might

be determining for vendace-bream/white bream- roach interactions. The obligate, zooplanktivorous vendace might use this food resource better than bream/white bream, which, in turn, use these copepods more efficiently than roach. Bream is probably more skillful than roach at catching copepods as these were more important food-source for small bream than they were for roach in Lake Trummen (Lessmark unpublished). This makes bream/white bream more competitive in deep lakes and roach more competitive in shallow lakes.

Thus the increasing number of competitors, mainly for roach, is one reason why the numerical proportion of perch to roach increased in the deeper lakes.

#### Diffuse competition

One may conclude that roach influence perch populations more than vice-versa because roach is the most abundant species, and that food-overlap between perch and roach monitor interspecific competition. However, this is a very static way of looking at competition, that does not take into account that competition is a dynamic process, and that species abundance and feeding at a specific time are results of previous competition.

Fish alter the structure, quality and quantity of the flora and fauna comprising their diet (see references in Lessmark 1983g). This in turn, influences interactions. Roach consume smaller prey than perch and reduce size of zooplankton, making them unprofitable to perch. Roach, but not perch, induced high biomass of blue-green algae in eutrophic lakes (G. Andersson et al. *Inst. of Limnology*, Lund, unpublished). This is of further competitive advantage to roach. This might indirectly reduce macrophyte vegetation, cause changes in the benthos, which is important food for perch. These diffuse competition mechanisms are, in my opinion, the most important factors favouring roach over perch.

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| Investigation<br>Year | Area (km <sup>2</sup> ) | Maximum depth<br>(m) | Mean depth<br>(m) | Epilimnion<br>depth (m) | Transparency<br>(m) | Phosphorus<br>(ug/l) | Blue-green<br>algae (mg/l) | Zooplankton<br>(crustaceans/l) | Cladoceran<br>size-class | Source                                              |
|-----------------------|-------------------------|----------------------|-------------------|-------------------------|---------------------|----------------------|----------------------------|--------------------------------|--------------------------|-----------------------------------------------------|
| Habo                  | 1977-78                 | 0.016                | 4.5               | 1.8                     | 2.5                 | 0.57                 | 72.1                       | 105                            | 3                        | G. Andersson unpubl.                                |
| Björnsjön             | 1974                    | 0.5                  | 4                 | 2                       | 4                   | 4                    | -                          | -                              | -                        | Lessmark 1976                                       |
| Läen                  | 1974                    | 10.3                 | 12                | 5                       | 10                  | 4                    | -                          | -                              | -                        | "                                                   |
| Lillesjön             | 1976                    | 0.042                | 4.2               | 2.0                     | 2.5                 | 2.5                  | 0                          | -                              | -                        | Ripl 1978                                           |
| Trekanten             | 1980-81                 | 0.134                | 6.7               | 4                       | 4                   | 1.0                  | 12.4                       | -                              | 1                        | Enell & Lundqvist<br>1983, Ripl &<br>Lundqvist 1977 |
| Laduviken             | 1980-81                 | 0.056                | 3                 | 2                       | 2                   | 0.8                  | 0                          | 426                            | 1                        | + unpubl. data<br>Ripl & Lundqvist<br>1977          |
| Långsjön              | 1976                    | 0.298                | 3                 | 2                       | 2.5                 | 0.6                  | 9.2                        | -                              | 1                        | G. Andersson unpubl.                                |
| Trummen               | 1980                    | 0.84                 | 2                 | 1.8                     | 2                   | 0.48                 | 5.9                        | 121                            | 1                        |                                                     |
| Sövdeborgs-<br>sjön   | 1975                    | 0.11                 | 3.5               | 2                       | 3.5                 | 1.55                 | -                          | 235                            | 1                        | unpublished data                                    |
| Sövdeborgs<br>sjön    | 1980                    | 0.11                 | 3.5               | 2                       | 3.5                 | 1.2                  | -                          | 166                            | 1                        | Persson 1983a                                       |
| Fegen                 | 1974                    | 23.6                 | 36                | 7.5                     | 9                   | 5.4                  | 0.01                       | 84                             | 1                        | Lundqvist 1975                                      |
| Kalvsjön              | 1974                    | 7.2                  | 21                | 6.2                     | 9                   | 4.3                  | 0.03                       | 67                             | 2                        | "                                                   |
| Flaten                | 1976                    | 0.63                 | 13.1              | 7.4                     | 6                   | 4.3                  | 0                          | -                              | 2                        | Ripl & Lundqvist<br>1977                            |
| Magelungen            | 1976                    | 2.29                 | 13.4              | 4.4                     | 4                   | 0.9                  | 10.0                       | -                              | 1                        | "                                                   |

Table 1. Limnological characteristics in summer for the 13 investigated south Swedish lakes.

Values for total phosphorus and biomass of blue-green algae are from the uppermost 2 m water layer. Epilimnion depth indicates depth of epilimnion with more than 2 mg oxygen per litre. Detailed information of the lakes is given in the references.



Table 2. List of fish species in the investigated lakes.

| FISH SPECIES                                | Habo | Björnsjön | Läen | Lillesjön | Trekanten | Laduviken | Långsjön | Trummen | Sövedborgssjön | Fegen | Kalvsjön | Flaten | Magelunden |
|---------------------------------------------|------|-----------|------|-----------|-----------|-----------|----------|---------|----------------|-------|----------|--------|------------|
| Perch ( <i>Perca fluviatilis</i> )          | +    | +         | +    | +         | +         | +         | +        | +       | +              | +     | +        | +      | +          |
| Roach ( <i>Rutilus rutilus</i> )            | +    | +         | +    | +         | +         | +         | +        | +       | +              | +     | +        | +      | +          |
| Pike ( <i>Esox lucius</i> )                 | +    | +         | +    | +         | +         | +         | +        | +       | +              | +     | +        | +      | +          |
| Crucian carp ( <i>Carassius carassius</i> ) |      |           |      | +         | +         | +         |          |         | +              |       | +        |        | +          |
| Rudd ( <i>Scardinius erythrophthalmus</i> ) |      |           | +    | +         |           |           |          | +       |                |       |          |        | +          |
| Bream ( <i>Abramis brama</i> )              |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| White bream ( <i>Blicca bjoerkna</i> )      |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Tench ( <i>Tinca tinca</i> )                |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Bleak ( <i>Alburnus alburnus</i> )          |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Pike-perch ( <i>Lucioperca lucioperca</i> ) |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Ruff ( <i>Acerina cernua</i> )              |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Whitefish ( <i>Coregonus</i> sp.)           |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Vendace ( <i>Coregonus albula</i> )         |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Eel ( <i>Anguilla anguilla</i> )            |      |           |      |           |           |           |          |         |                |       |          |        | +          |
| Carp ( <i>Cyprinus carpio</i> )             | +    | +         | +    |           | +         |           |          | +       | +              | +     | +        |        |            |
| Gudgeon ( <i>Gobio gobio</i> )              |      |           |      |           |           |           |          |         |                |       |          |        |            |
| Burbot ( <i>Lota lota</i> )                 |      |           |      |           |           |           |          |         |                |       |          |        |            |
| Sculpin ( <i>Cottus gobio</i> )             |      |           |      |           |           |           |          |         |                |       |          |        |            |
| "Minnow" ( <i>Leucaspius delineatus</i> )   |      |           |      |           |           |           |          |         |                |       |          |        |            |

Table 3. Size-class diversity (Shannon-Wiener index) and mean length of perch and roach in 12 south Swedish lakes.

| Lake                | Diversity |       | Mean length |       |
|---------------------|-----------|-------|-------------|-------|
|                     | Perch     | Roach | Perch       | Roach |
| Björnsjön           | 3.74      | -     | 177         | -     |
| Läen                | 3.09      | -     | 144         | -     |
| Lillesjön           | -         | 3.46  | -           | 141   |
| Trekanten           | 4.06      | 1.99  | 185         | 100   |
| Laduviken           | 3.76      | 3.71  | 149         | 129   |
| Långsjön            | 3.50      | 2.37  | 129         | 101   |
| Trummen             | 2.80      | 2.54  | 99          | 115   |
| Sövdeborgssjön 1975 | 3.14      | 3.68  | 134         | 155   |
| Sövdeborgssjön 1980 | 2.42      | 2.45  | 95          | 108   |
| Fegen               | 3.31      | 3.48  | 157         | 177   |
| Kalvsjön            | 2.92      | 3.41  | 154         | 153   |
| Flaten              | 3.67      | 4.04  | 174         | 182   |
| Magelungen          | 3.65      | 3.12  | 131         | 115   |

Table 4. Food of perch and roach of different size-classes in Lakes Trekanten, Laduviken, Trummen and Pond Habo.

| LAKE           | PERCH                                       |                                          | ROACH                   |                           |
|----------------|---------------------------------------------|------------------------------------------|-------------------------|---------------------------|
|                | size-class, cm                              | Dominating food items                    | Dominating food items   | Others                    |
| <hr/>          |                                             |                                          |                         |                           |
| Trekanten      |                                             |                                          |                         |                           |
| 5-9.9          | -                                           | -                                        | cladocerans             | -                         |
| 10-14.9        | copepods<br>chironomids<br><u>Chaoborus</u> | -                                        | detritus                | chironomids               |
| 15-19.9        | -                                           | -                                        | detritus                | chironomids               |
| 20-            | roach                                       | -                                        | detritus                | -                         |
| <hr/>          |                                             |                                          |                         |                           |
| Laduviken 1980 |                                             |                                          |                         |                           |
| 5-9.9          | copepods                                    | -                                        | cladocerans             | detritus<br>algae, plants |
| 10-14.9        | chironomids                                 | <u>Lepto-</u><br><u>dora</u><br>copepods | macroalgae<br>detritus  | cladocerans<br>copepods   |
| 15-            | -                                           | -                                        | detritus                | -                         |
| <hr/>          |                                             |                                          |                         |                           |
| Laduviken 1981 |                                             |                                          |                         |                           |
| 5-9.9          | roach                                       | -                                        | <u>Bosmina</u>          | detritus                  |
| 10-15.9        | roach                                       | chironomids                              | detritus                | <u>Bosmina</u>            |
| 15-19.9        | roach                                       | -                                        | detritus                | -                         |
| 20-            | roach                                       | -                                        | -                       | -                         |
| <hr/>          |                                             |                                          |                         |                           |
| Trummen        |                                             |                                          |                         |                           |
| 5-9.9          | chironomids                                 | insect-<br>larvae<br>zooplank-<br>ton    | detritus<br>cladocerans |                           |
| 10-14.9        | fish<br>insect larvae                       | zoo-<br>plankton                         | detritus<br>cladocerans |                           |
| 15-            | fish                                        | -                                        | detritus<br>cladocerans | -                         |
| <hr/>          |                                             |                                          |                         |                           |
| Habo           |                                             |                                          |                         |                           |
| 10-29.9        | cladocerans                                 |                                          | cladocerans             |                           |
| <hr/>          |                                             |                                          |                         |                           |

| Perch 2 year       | Abundance, perch | Abundance, roach | Abundance, all fish | Number of fish species | Mean length, perch | Mean length, roach | Diversity, perch | Diversity, roach | Maximum depth | Mean depth | Epilimnion depth | Area | Transparency | Phosphorus, concentration | Size class, zooplankton | Abundance, crustaceans | Biomass, blue-green algae |
|--------------------|------------------|------------------|---------------------|------------------------|--------------------|--------------------|------------------|------------------|---------------|------------|------------------|------|--------------|---------------------------|-------------------------|------------------------|---------------------------|
| 4                  | 12               | 13               | 06                  | 00                     | 41                 | 00                 | 56               | 00               | 01            | 01         | 08               | 10   | 10           | 59                        | 32                      | 03                     | 46                        |
| 6                  | 30               | 08               | 11                  | 00                     | 17                 | 16                 | 61               | 22               | 02            | 02         | 18               | 18   | 35           | 27                        | 14                      | -                      | 14                        |
| Roach 2            | 07               | 06               | 00                  | 16                     | 07                 | 07                 | 06               | 09               | 07            | 13         | 13               | 11   | 03           | 08                        | 52                      | 16                     | 06                        |
| 4                  | 12               | 04               | 00                  | 15                     | 02                 | 08                 | 04               | 10               | 04            | 10         | 10               | 10   | 05           | 07                        | 64                      | 14                     | 04                        |
| 6                  | 08               | 75               | 55                  | 04                     | 00                 | 73                 | 26               | 82               | 02            | 12         | 05               | 02   | 44           | 70                        | 50                      | -                      | 89                        |
| 8                  | 30               | 96               | 54                  | 05                     | 00                 | 88                 | 51               | 93               | 04            | 19         | 09               | 01   | 54           | 76                        | 59                      | -                      | 88                        |
| Abundance perch    | -                | 13               | 00                  | 07                     | 00                 | 02                 | 00               | 04               | 04            | 06         | 02               | 00   | 01           | 12                        | 15                      | 00                     | 11                        |
| Abundance roach    | 13               | -                | 84                  | 05                     | 41                 | 55                 | 01               | 43               | 45            | 55         | 58               | 26   | 56           | 24                        | 31                      | 00                     | 29                        |
| Mean length, perch | 00               | 41               | 48                  | 00                     | -                  | 18                 | 60               | 09               | 10            | 23         | 12               | 02   | 28           | 00                        | 18                      | 01                     | 02                        |
| Mean length, roach | 02               | 55               | 54                  | 09                     | 18                 | -                  | 00               | 00               | 39            | 47         | 43               | 28   | 76           | 65                        | 34                      | 08                     | 68                        |
| Diversity perch    | 00               | 01               | 02                  | 00                     | 60                 | 00                 | -                | 00               | 00            | 02         | 03               | 02   | 00           | 20                        | 00                      | 40                     | 14                        |
| Diversity roach    | 04               | 43               | 37                  | 05                     | 09                 | 00                 | 00               | -                | 11            | 16         | 11               | 05   | 34           | 43                        | 24                      | 16                     | 75                        |
| Dominance roach    | 01               | 58               | 59                  | 06                     | 16                 | 68                 | 00               | 39               | 56            | 37         | 60               | 57   | 68           | 52                        | 14                      | 11                     | 56                        |

Table 5. Values for the coefficient of determination ( $r^2$ ) x 100 for the linear regressions for fish population characteristics and abiotic and biotic factors in 13 south Swedish lakes. Underlined values indicate negative relationships.

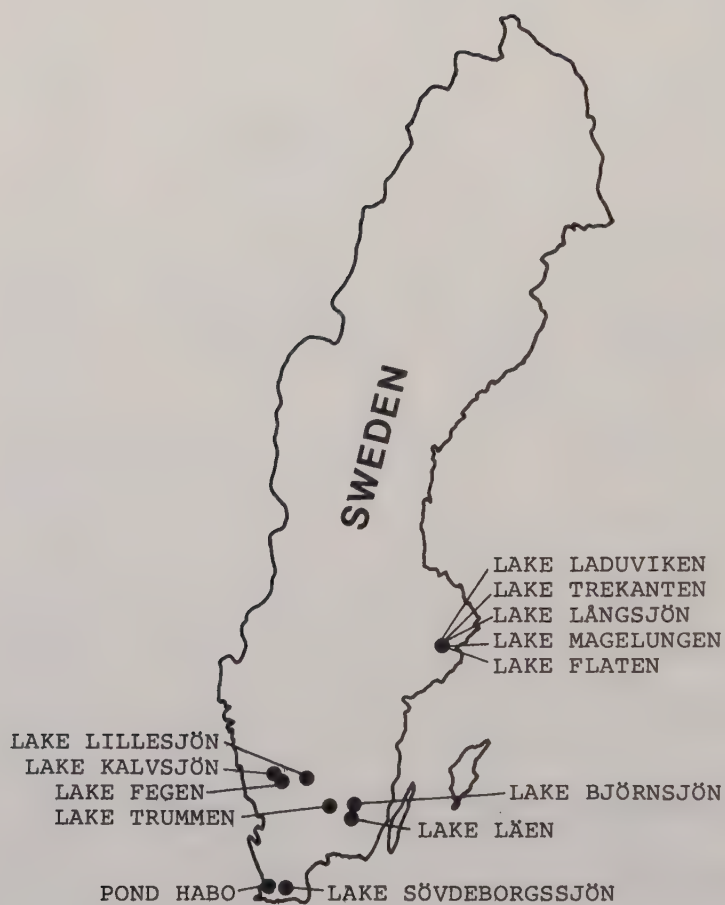


Fig. 1. Location of the 13 investigated lakes.



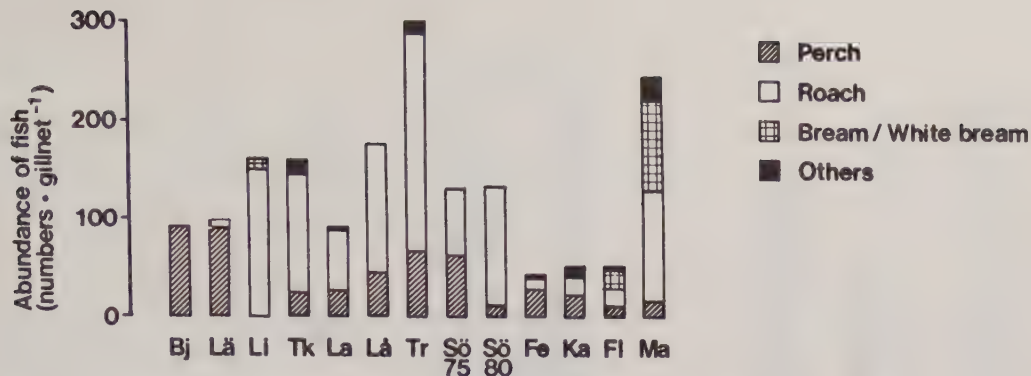


Fig. 2. Relative abundance of fish in the epilimnion of the investigated lakes. (Bj = Lake Björnsjön, LÄ = L.Läen, LI = L.Lillesjön, Tk = L.Trekanten, La = L.Laduviken, LÅ = L. Långsjön, Tr = L. Trummen, Sö75 and Sö80 = L.Sövdeborgssjön in 1975 respectively 1980, Fe = L.Fegen, Ka = L. Kalvsjön, Fl = L. Flaten, Ma = L. Magelungen) (Values for L. Sövdeborgssjön in 1980 not directly comparable to the others since a different kind of gill-nets were used)

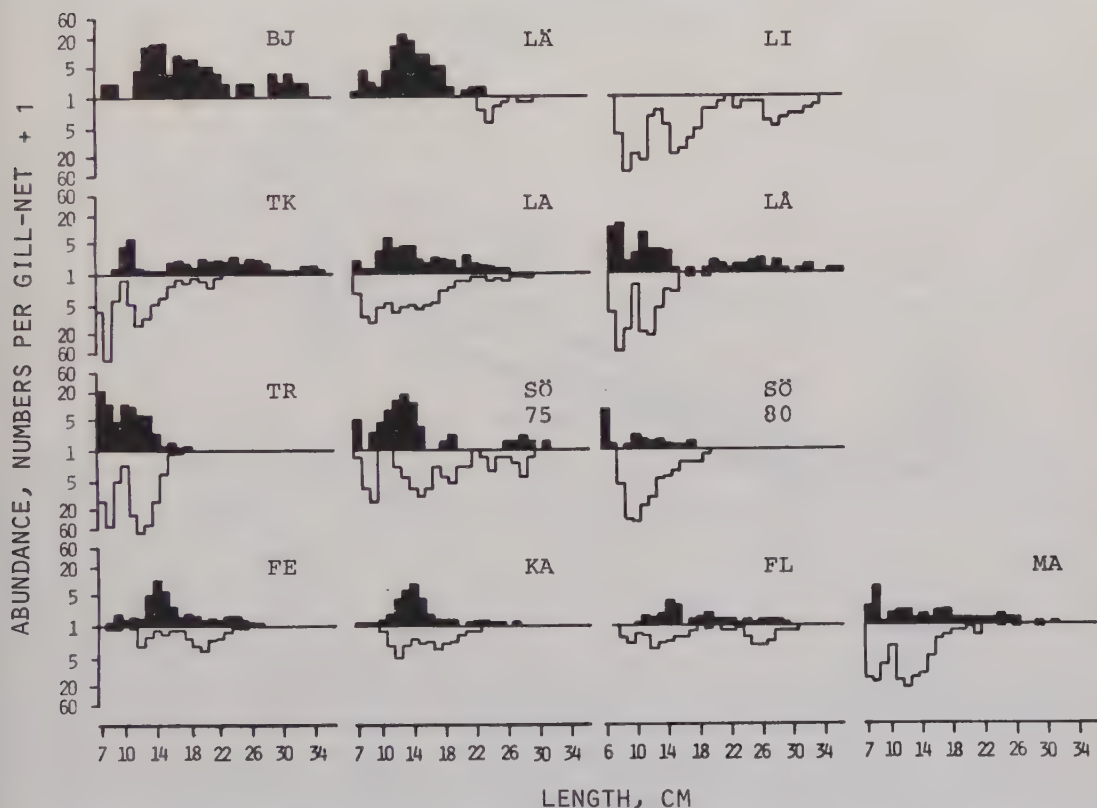


Fig. 3. Size-class distribution of perch and roach in the investigated lakes. Black columns indicate perch, white roach. Abbreviations of lake names as in figure 2.

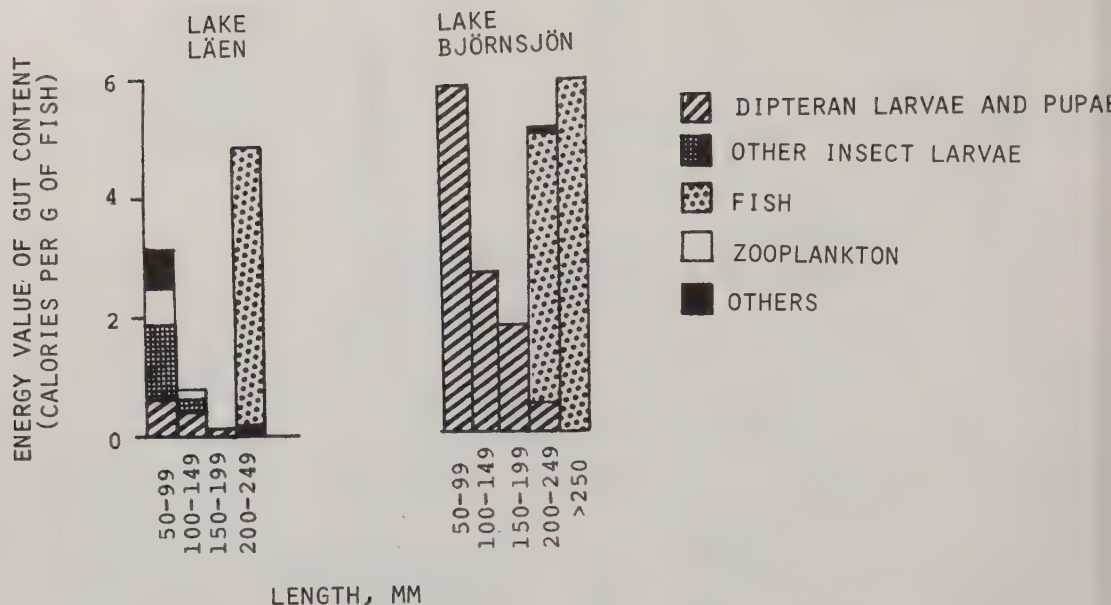


Fig. 4. Energy value of gut content of perch of different size-classes in Lakes Län and Björnsjön.

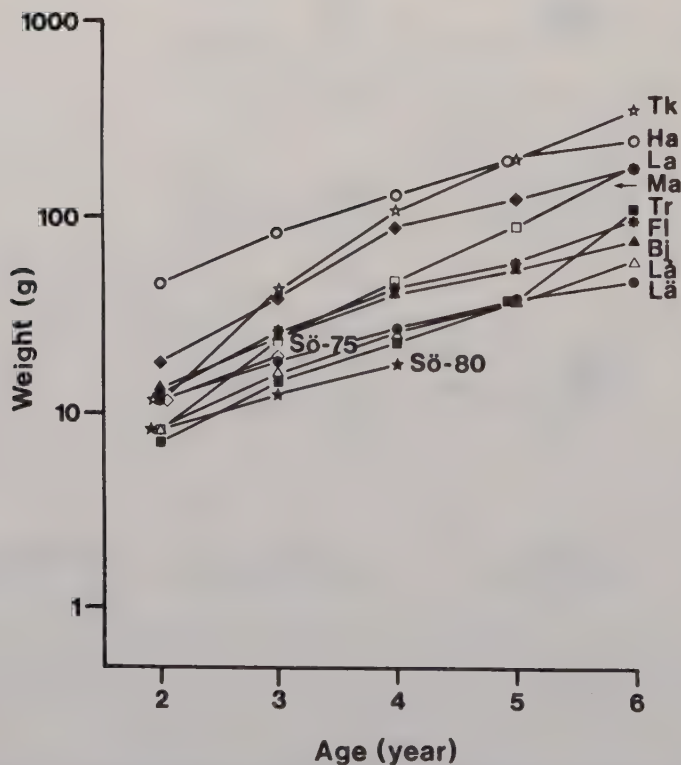


Fig. 5. Growth of perch in the investigated lakes, expressed as mean weight at different ages. Ha = Pond Habo. Other abbreviations as in figure 2.

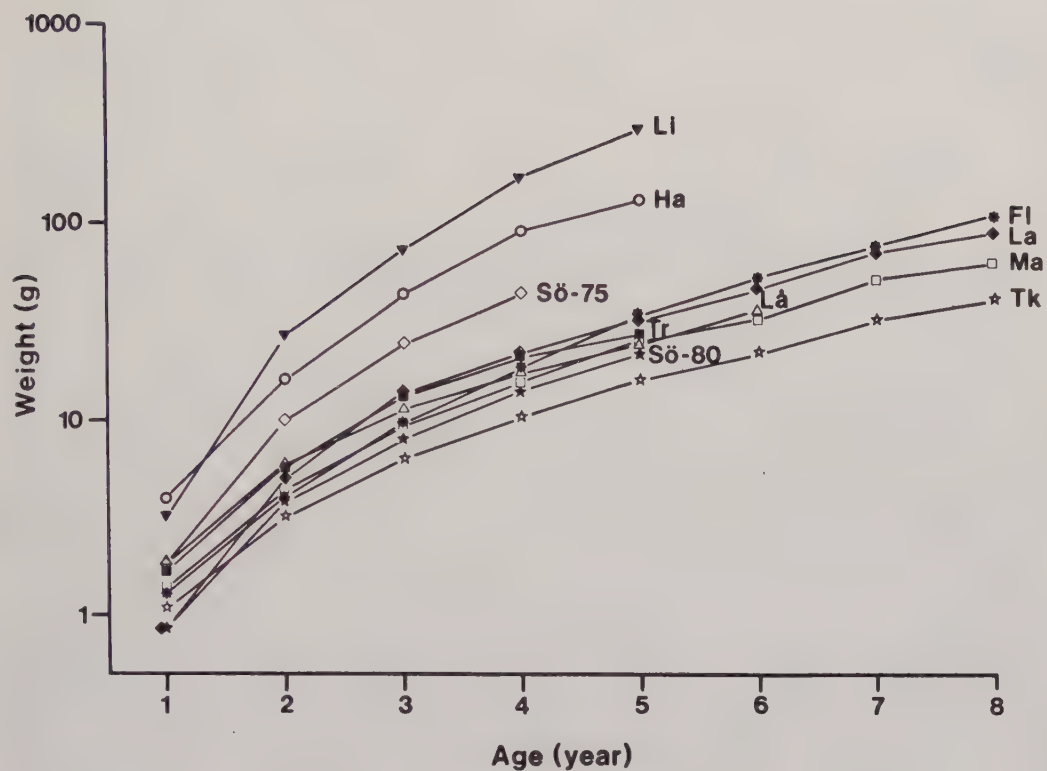


Fig. 6. Growth of roach in the investigated lakes expressed as mean weight at different ages. Abbreviations as in figure 2 and 5.

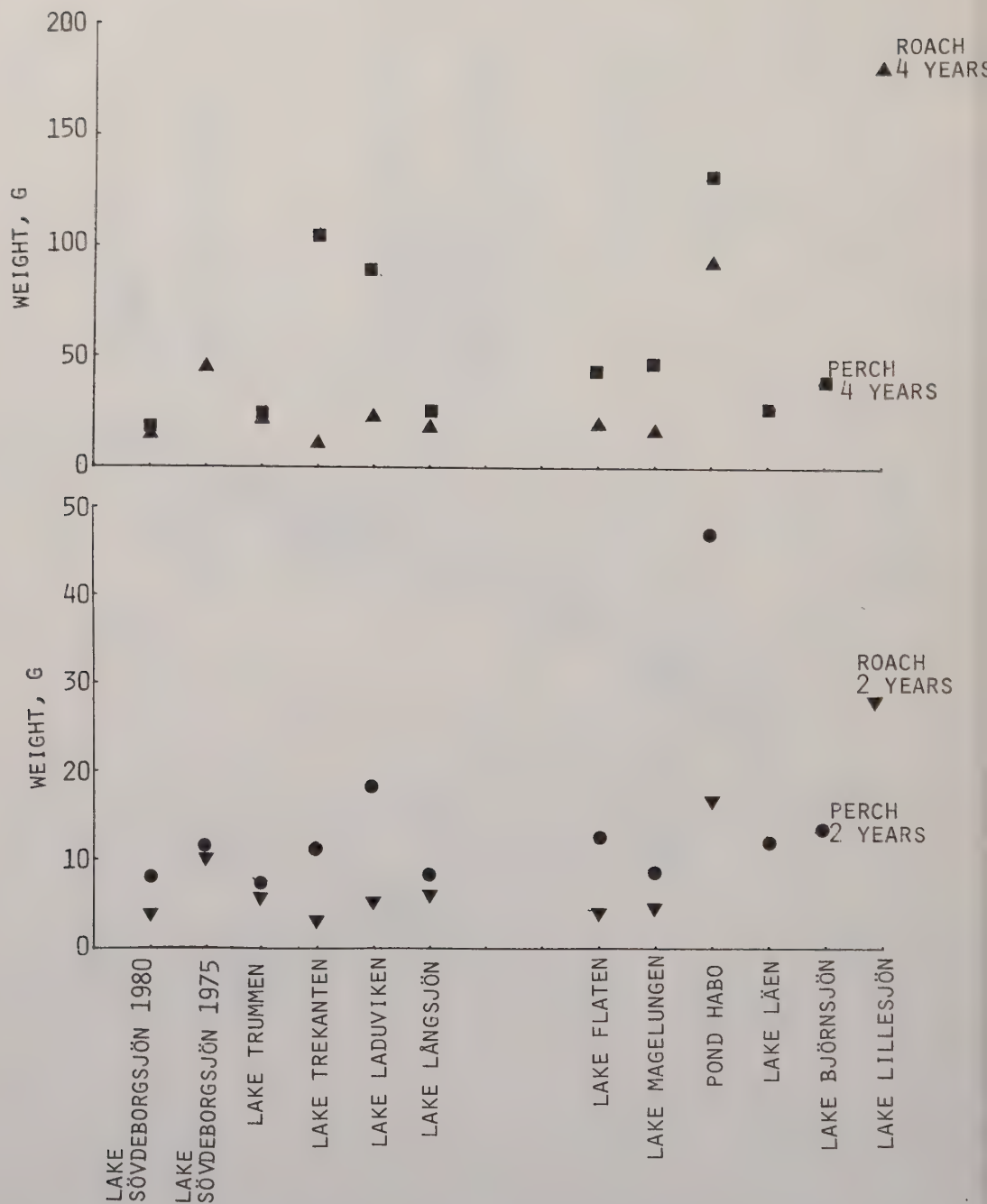


Fig. 7. Weight of perch and roach at 2 and 4 years age in the investigated lakes.

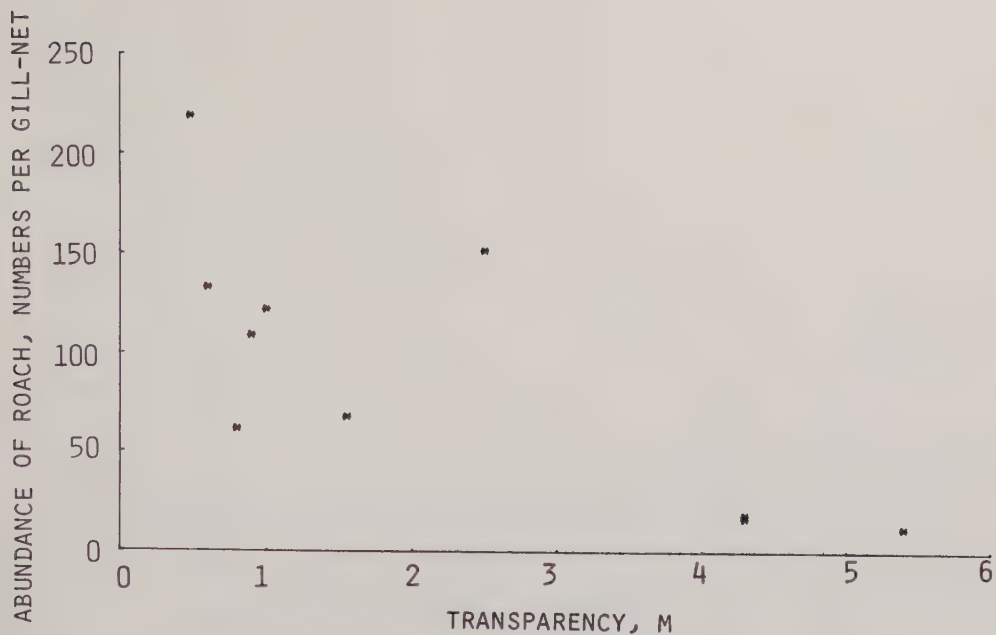


Fig. 8. Relation between abundance of roach and transparency in 10 south Swedish lakes.

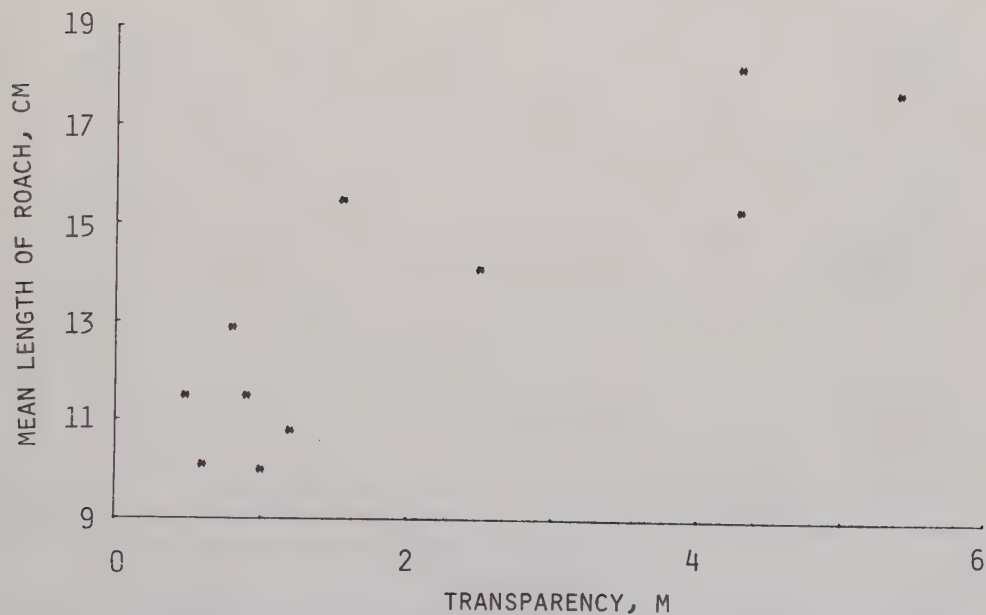


Fig. 9. Relation between mean length of roach and transparency in 11 south Swedish lakes.



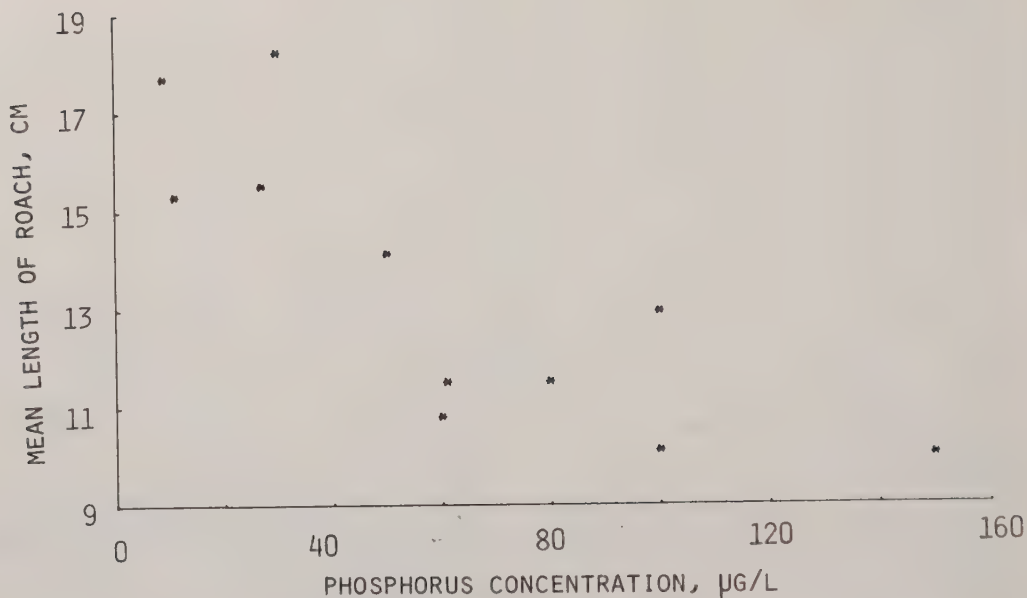


Fig. 10. Relation between mean length of roach and total phosphorus concentration in the water in 11 south Swedish lakes.

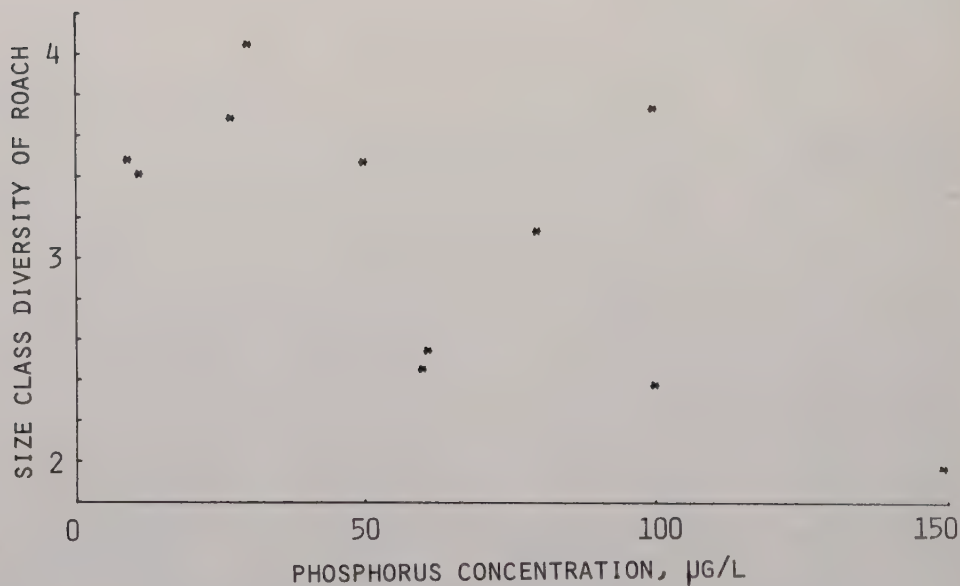


Fig. 11. Relation between size-class diversity (Shannon-Wiener index) of roach and total phosphorus concentration in the water in 11 south Swedish lakes.



Fig. 12. Relation between size-class diversity (Shannon-Wiener index) of roach and transparency in 11 south Swedish lakes.

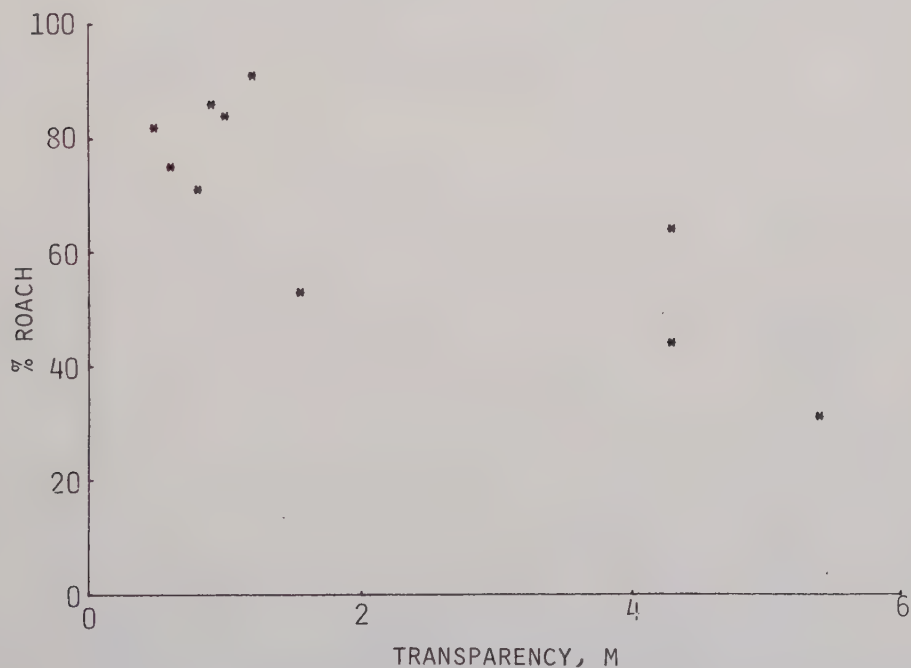


Fig. 13. Relation between roach dominance (measured as percentage proportion of roach of the total abundance of roach plus perch) and transparency in 10 south Swedish lakes.

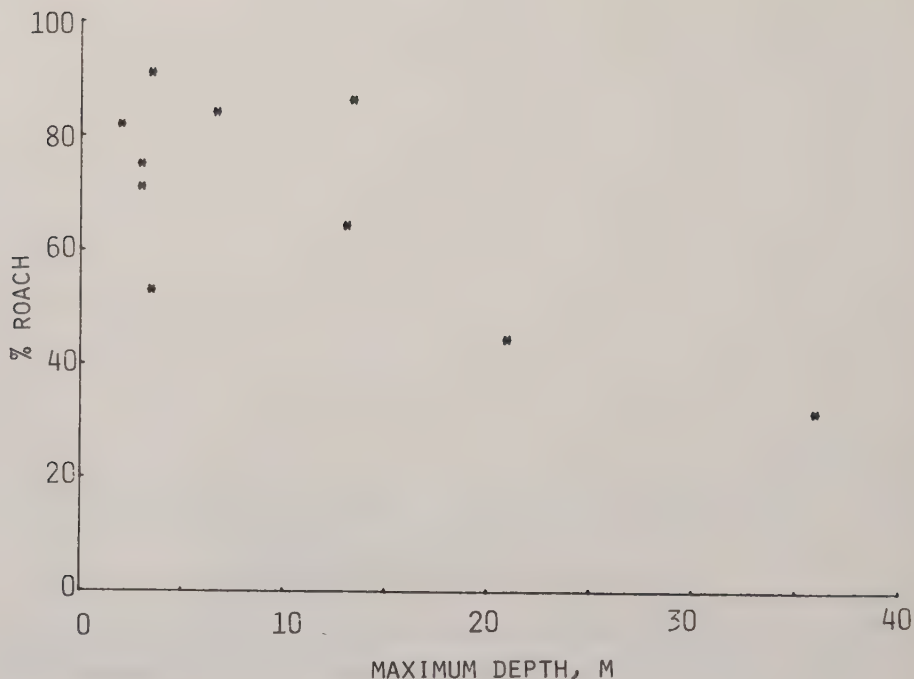


Fig. 14. Relation between roach dominance (for explanation see figure 13) and maximum depth in 10 south Swedish lakes.

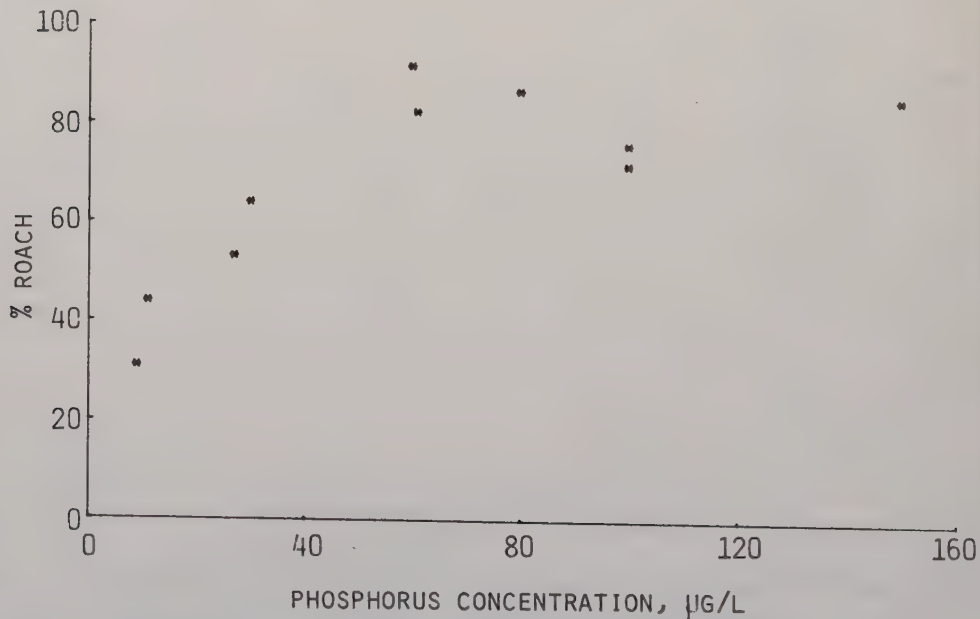


Fig. 15. Relation between roach dominance (for explanation see figure 13) and total phosphorus concentration in the water in 10 south Swedish lakes.

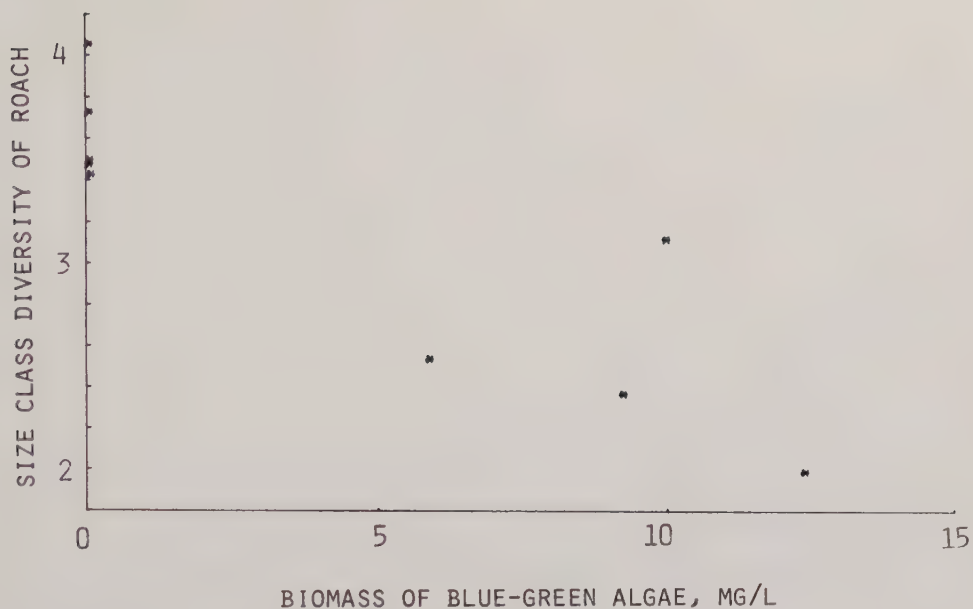


Fig. 16. Relation between size-class diversity (Shannon-Wiener index) of roach and biomass of blue-green algae in 9 south Swedish lakes.

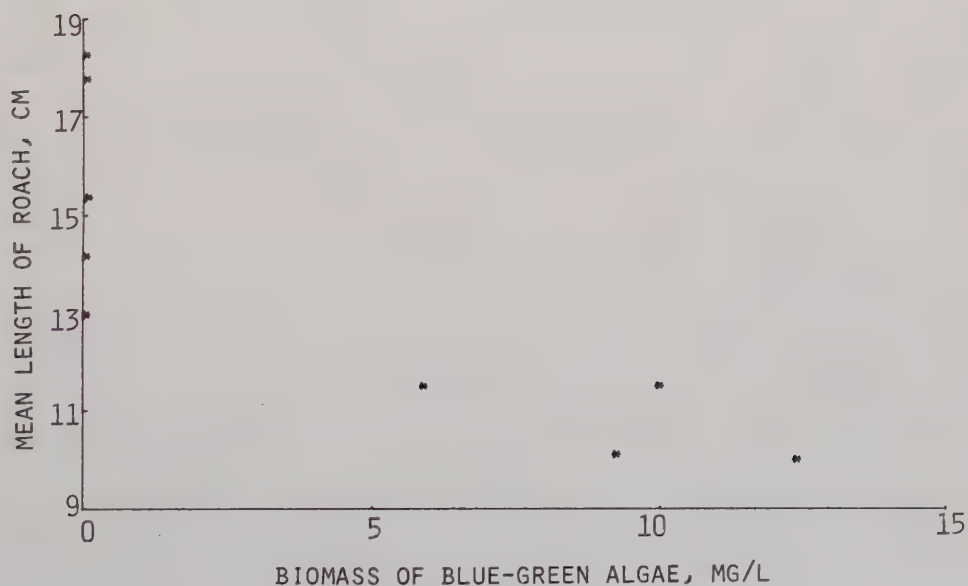


Fig. 17. Relation between mean length of roach and biomass of blue-green algae in 9 south Swedish lakes.

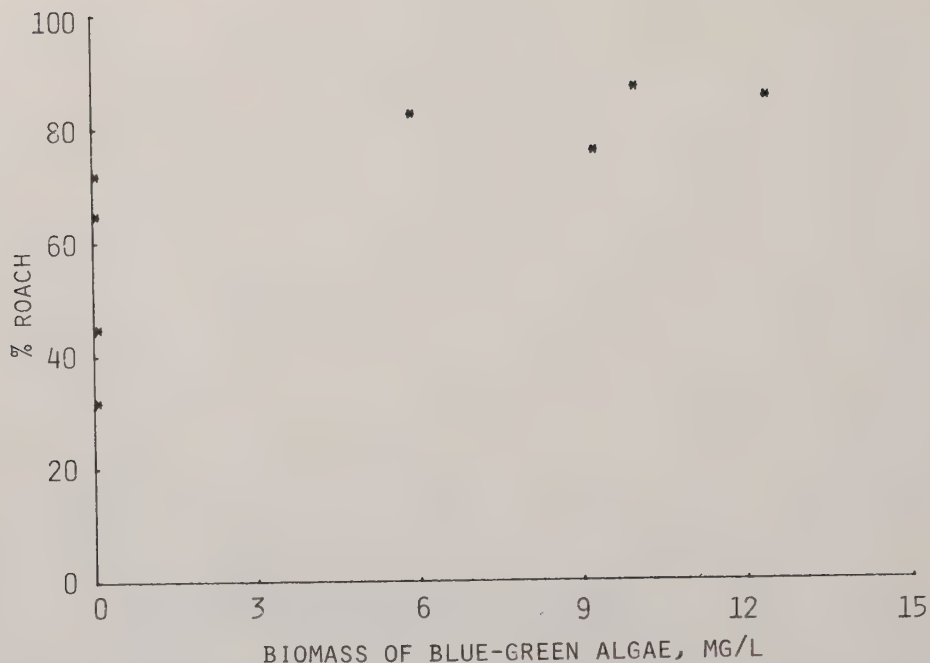


Fig. 18. Relation between roach dominance (measured as percentage proportion of roach of the total abundance of roach plus perch) and biomass of blue-green algae in 8 south Swedish lakes.

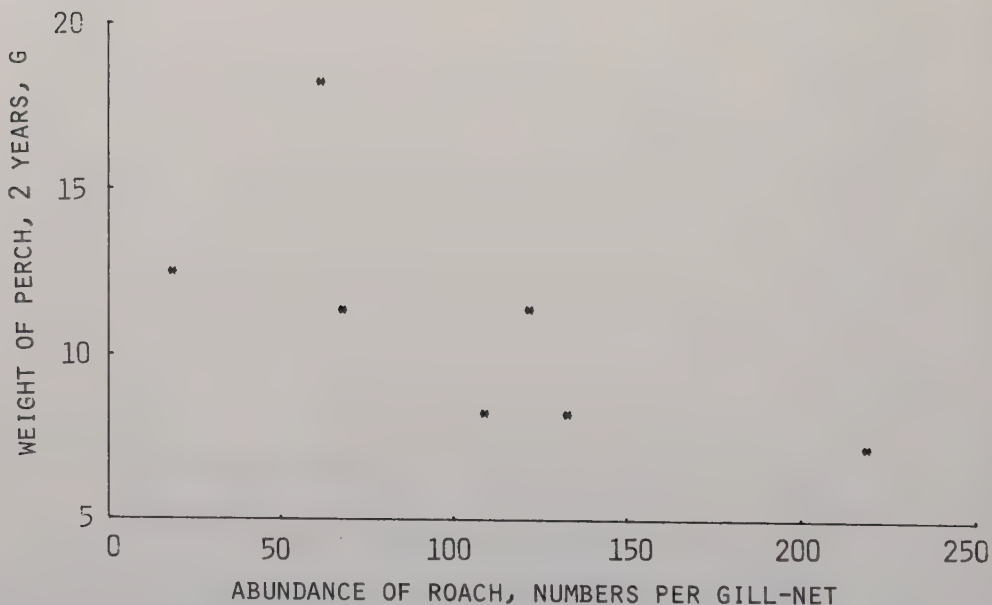


Fig. 19. Relation between mean weight of perch at 2 years age and abundance of roach in 7 south Swedish lakes.



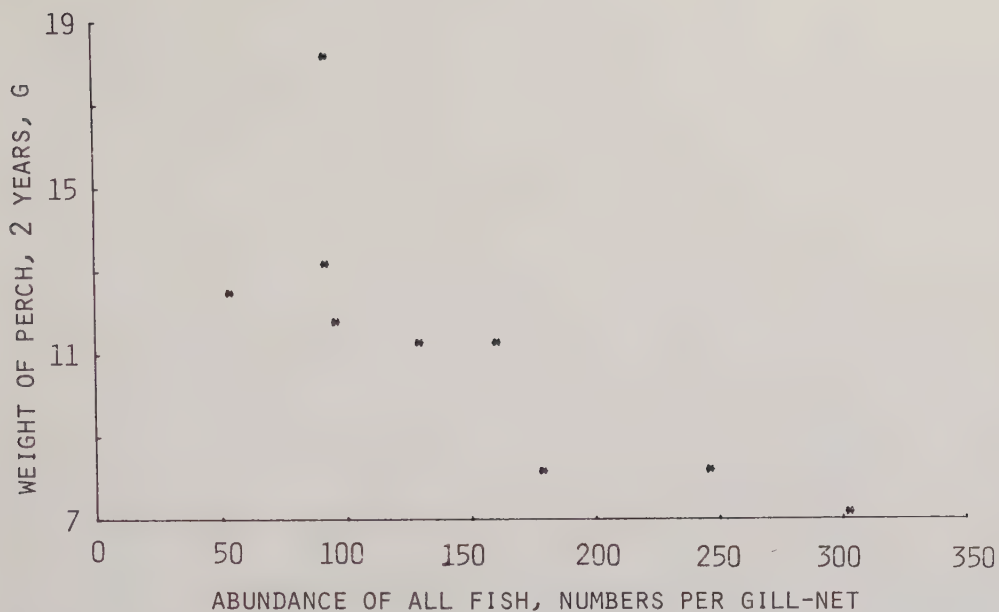


Fig. 20. Relation between mean weight of perch at 2 years age and total abundance of fish in 9 south Swedish lakes.

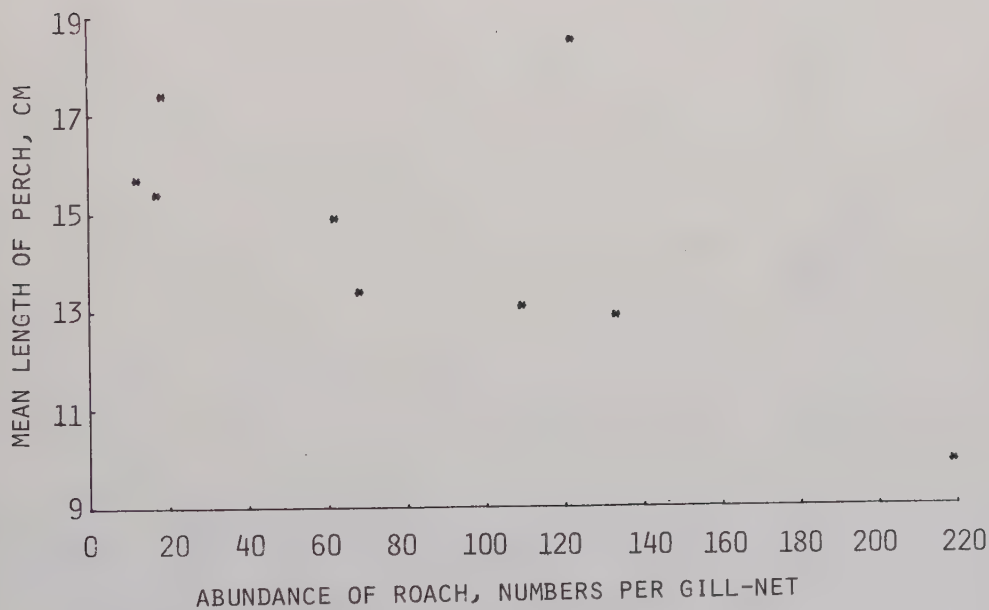


Fig. 21. Relation between mean length of perch and abundance of roach in 9 south Swedish lakes.

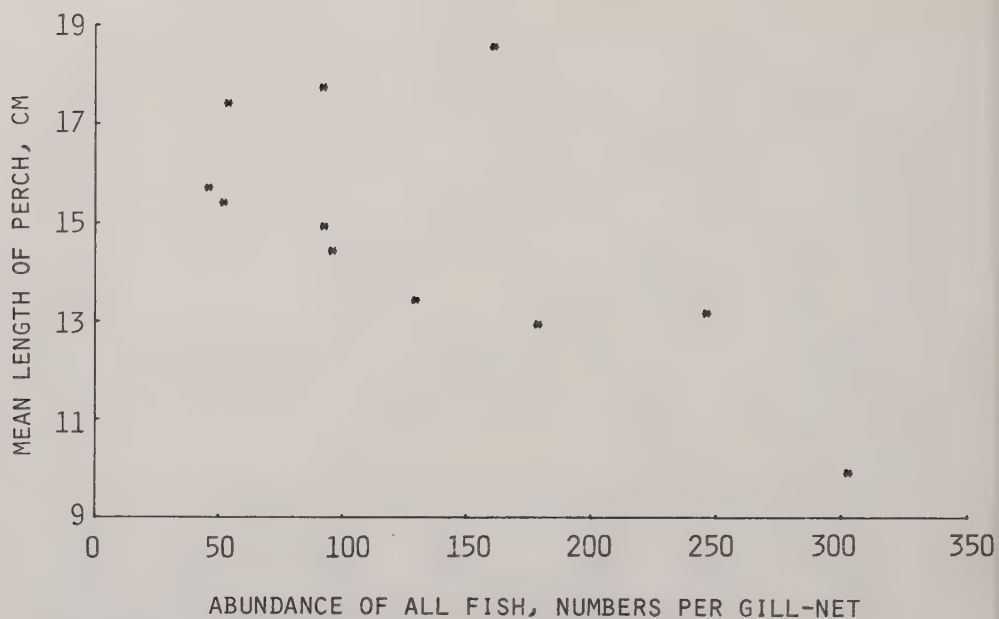


Fig. 22. Relation between mean length of perch and total abundance of fish in 11 south Swedish lakes.

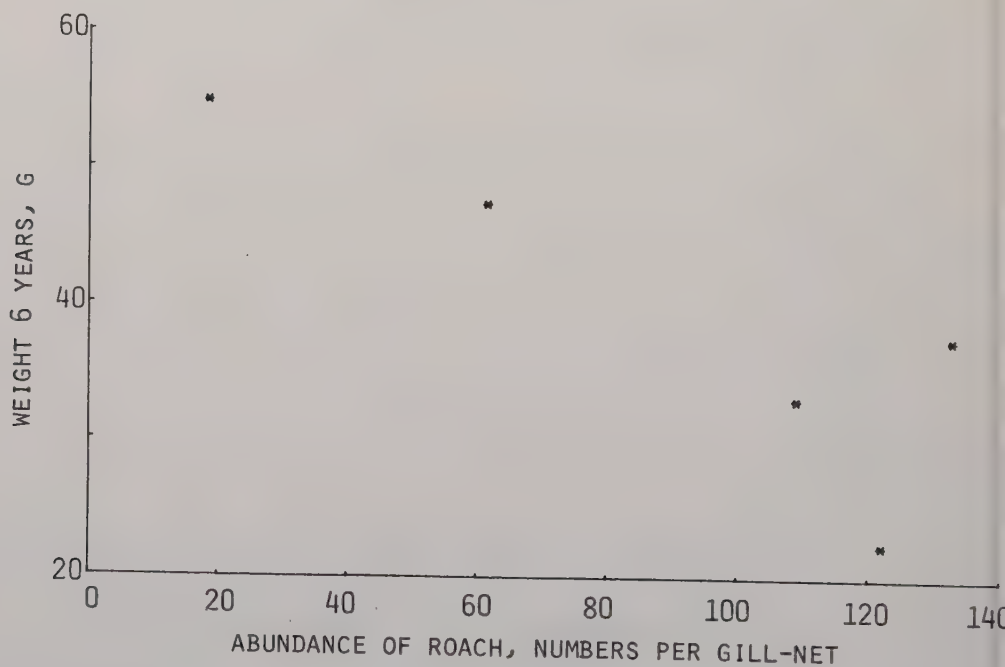


Fig. 23. Relation between mean weight of roach at 6 years age and abundance of roach in 5 south Swedish lakes.

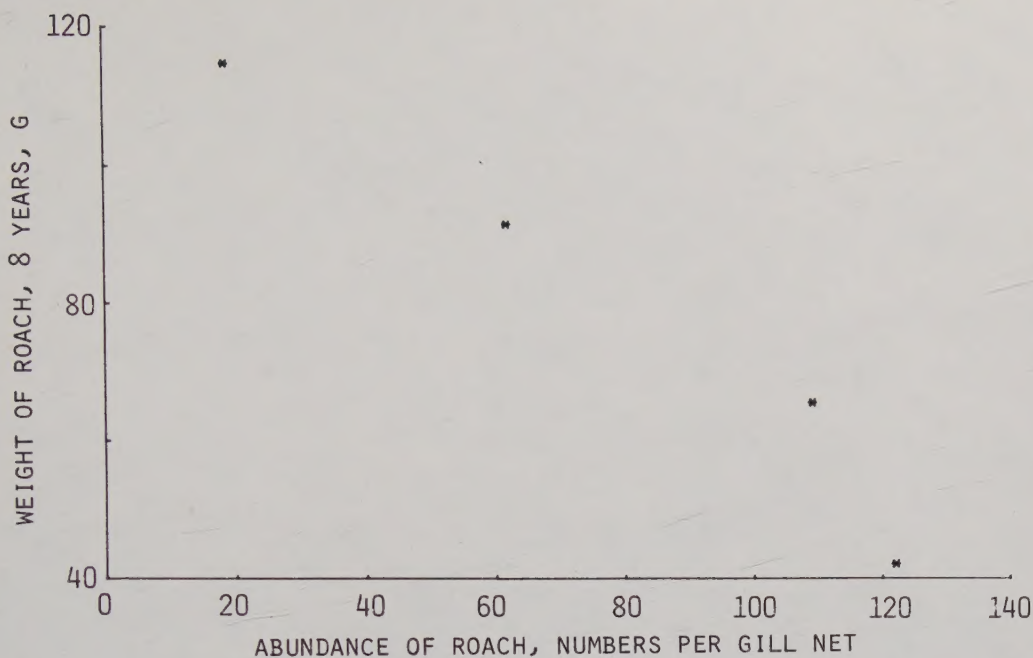


Fig. 24. Relation between mean weight of roach at 8 years age and abundance of roach in 4 south Swedish lakes.

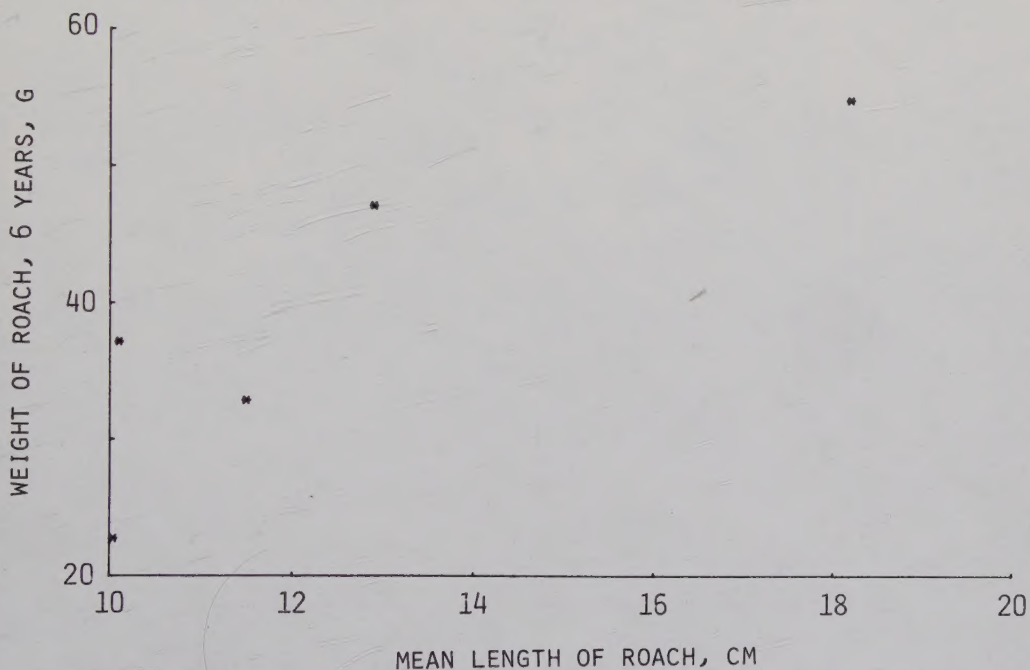


Fig. 25. Relation between mean weight of roach at 6 years age and mean length of roach in 5 south Swedish lakes.

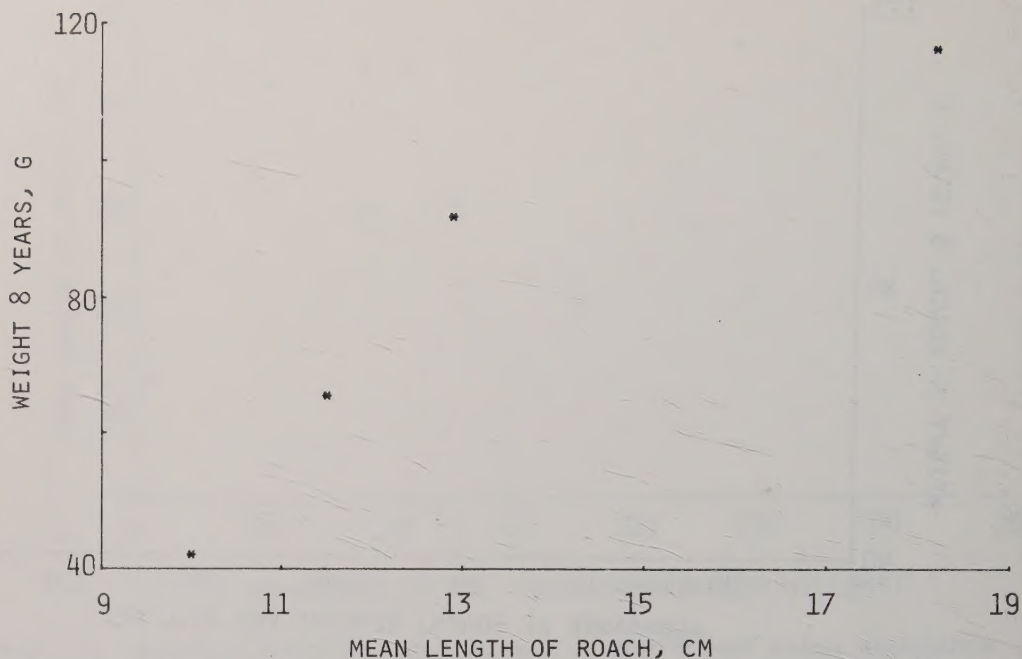


Fig. 26. Relation between mean weight of roach at 8 years age and mean length of roach in 4 south Swedish lakes.

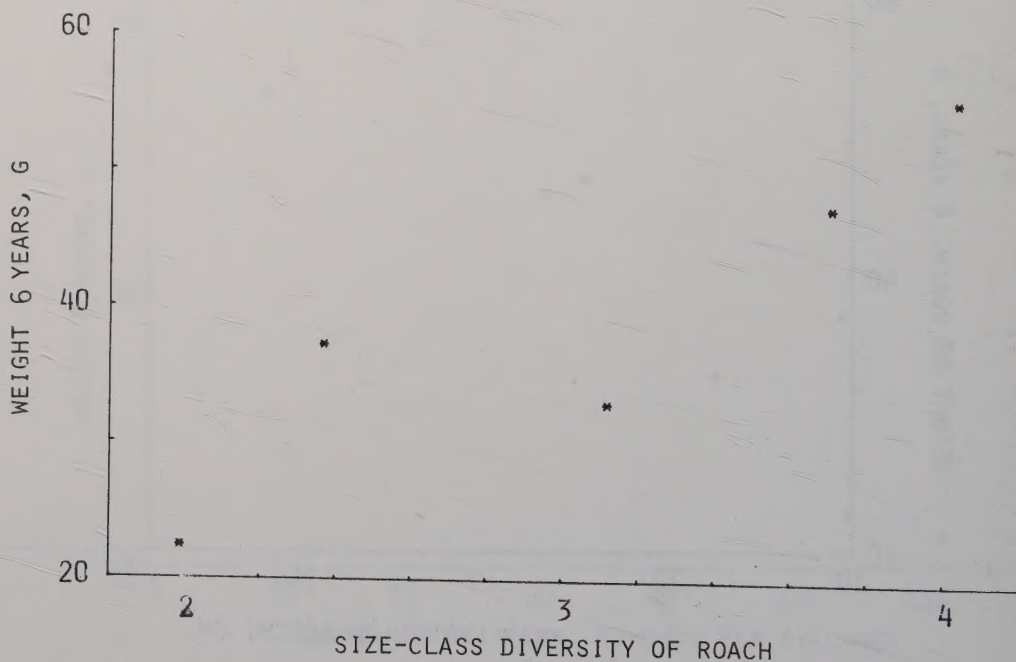


Fig. 27. Relation between mean weight of roach at 6 years age and size-class diversity (Shannon-Wiener index) of roach in 4 south Swedish lakes.







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